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THE DIVISIONS AND CLASSES OF PLANTS
Arthur Cronquist

ECOLOGICAL EFFECTS OF FOREST FIRES
I. F. Ahlgren and C. E. Ahlgren

THE CLIMAX CONCEPT
G. W. Selleck

BIOLOGICAL ANTAGONISMS DUE TO PHYTOTOXIC ROOT EXUDATES
Frank W. Woods

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THE DIVISIONS AND CLASSES OF PLANTS

ARTHUR CRONQUIST

The New York Botanical Garden

Introduction 426

Preliminary Considerations 427

Definition of the Plant Kingdom 427

The Subkingdoms 433

Endings of Names of Classes 433

Synopsis of the Divisions and Classes of Plants 436

Outline of the Classification of the Plant Kingdom 445

Discussion 447

Bacteria 447

Blue-green Algae 449

Red Algae 451

Flagellates and Their Algal Descendants 452

Fungi 459

General Features of Embryophytes 465

Bryophytes 467

Vascular Plants 469

Conclusion 477

Bibliography 478

INTRODUCTION

The familiar system of classification in which the plant kingdom is parceled into four divisions (Thallophyta, Bryophyta, Pteridophyta, Spermatophyta) has outlived its usefulness and is now disappearing from textbooks. Algologists unanimously proclaim that the algae comprise several distinct divisions, some of which are not very closely allied to each other. Mycologists consider the fungi to represent one or more divisions. Some students of the vascular plants recognize for this group a single division, Tracheophyta or Stelophyta, while others recognize several, but there is growing agreement that in any case the traditional classification of all vascular plants into the divisions Pteridophyta and Spermatophyta is unsound.

A number of systems incorporating recent knowledge and viewpoints have appeared, but most of these deal with only limited segments of the plant kingdom, or are mere skeletons without explanatory comments, or are revised only in certain areas, retaining the outmoded concepts in other areas. The most interesting recent complete treatment which has come to my attention is that of Nemejc (1950). I agree with a great deal of Nemejc's comment, especially as regards the vascular plants. Unfortunately, as is noted in my discussion of the gymosperms, his system does not fully reflect his accompanying argument. Furthermore, the thallophytes, being less amenable to the paleontological approach which he stresses, are less adequately treated. Recent evidence from flagellar structure, pigmentation and food reserves, among other things, should permit a more satisfactory arrangement.

The present paper is an attempt to make use of the information and thought now available in order to achieve a coherent natural system for the plant kingdom as a whole, and to explain the reasons for some of the conclusions. No attempt is made to present an exhaustive bibliography; individual papers are cited only insofar as they are pertinent to the discussion, especially to indicate some of the evidence on which my views are based, and to document information that may not be universally familiar. The phylogenetic chart was designed by my son, John Cronquist, under my supervision. Drs. H. W. Blaser, C. L. Hitchcock, D. D. Keck and R. M. Klein have read the manuscript and offered useful suggestions. I am grateful for their assistance.

PRELIMINARY CONSIDERATIONS

DEFINITION OF THE PLANT KINGDOM

The first question to be faced is the definition of the plant kingdom. It is generally realized that no sharp distinction can be drawn between plants and animals, and that the unicellular flagellates in particular include many dubious or transitional forms. This difficulty has led to a number of attempts to recognize three or more often four kingdoms of organisms. Unfortunately, an attempt to recognize four kingdoms instead of two presents us with the necessity to draw three hazy lines instead of only one. Four-kingdom systems avoid some of the problems with the flagellates, but they have additional difficulties of their own. Although each of the several four-kingdom systems referred to below is different from the others, all have the common fault of not solving the basic problem which brought them into being.

The most notable recent four-kingdom systems are those of Copeland (1938, 1956), Barkley (1939), Rothmaler (1948, 1951) and Whittaker (1959). Copeland presents a logical argument for including the green algae in his kingdom Plantae, but Barkley and Rothmaler refer the green algae to another kingdom, variously called Protista (the most familiar name), Protoctista, or Protobionta. All these authors except Whittaker include the red algae in the kingdom Protista (under one or another name) where they have no close relatives. The real relationships of the red algae are with the blue-green algae, which are referred to another kingdom variously called Monera, Anucleobionta, or Mychota.

Whittaker's system has the special distinction of having a kingdom Plantae which is polyphyletic. He refers the red algae, brown algae, green algae and all the embryophytes to his kingdom Plantae, whereas the bacteria, blue-green algae and all the flagellates except the green algal ones are referred to his kingdom Protista. As shown in my accompanying chart, the brown algae can be related to the eventually ancestral green algae only through flagellated ancestors which would have to be referred to Whittaker's Protista. Thus we would have an evolutionary line from Protista (bacteria and blue-green algae) to Plantae (green algae) to Protista (nonchlorophycean flagellates) to Plantae (brown algae). If the evolutionary concepts presented in this paper bear any relationship to the truth, Whittaker's arrangement is wholly unsatisfactory.

Copeland's system, being more detailed than the others, exposes the

inherent difficulties of a four-kingdom arrangement even more clearly. According to Copeland's own studies (1955) on the cytology of *Prasiola,* this algal genus should belong to his kingdom Mychota, organisms without typical nuclei. In 1956, however, he included it in his kingdom Protoctista, phylum Rhodophyta (red algae). Most algologists have considered *Prasiola* to belong to the Chlorophyceae, as would be indicated by its pigments. Studies by Friedmann (1960) show that at least some species of *Prasiola* have normal sexual processes, and inferentially that they have vesicular nuclei like those of other green (and red) algae. The spores of *Prasiola,* moreover, resemble vegetative cells of *Trebouxia,* a green algal genus of the order Chlorococcales. This forlorn little genus, which in the traditional system is clearly a plant, is now lost among three kingdoms. It is of course true that the same questions as to the affinities of this or any other doubtful genus must be met, regardless of the taxonomic rank at which the various groups are received, but the point is that the difficulties in a two-kingdom system are not resolved by changing to a four-kingdom system.

Even among the flagellates Copeland's system does not avoid all difficulties. Flagellates of the chlorophycean family Polyblepharidaceae lack a cell wall and should, therefore, belong to his kingdom Protoctista, but their omission from his detailed synopsis of this kingdom (1956) suggests that he is leaving them with the Chlorophyceae in the kingdom Plantae. The Polyblepharidaceae are, in fact, regularly included in the Chlorophyceae by algologists; except for the absence of a cell wall, some members of this family are very much like the familiar green algal genus *Chlamydomonas.*

Thus, although a four-kingdom system has some advantages, it still does not avoid the necessity to draw arbitrary lines, and in at least some respects it is less natural than a two-kingdom system. The two traditional and still useful kingdoms, therefore, should not be replaced by four kingdoms.

How, then, may the two kingdoms of organisms best be defined? The textbook lists of differences between plants and animals, based largely on higher plants and higher animals, are too well known to require repetition here. The several differences commonly listed in the textbooks are all related eventually to the basic difference in mode of nutrition: Most animals ingest their food, whereas most plants make their own. Starting with relatively undifferentiated unicellular organ-

isms, three general modes of nutrition are available: autotrophic, holozoic and chylotrophic[1]. Phylads which adopted the autotrophic mode evolved a set of characters associated with that mode and are called plants. Phylads which adopted the holozoic mode developed a set of characters associated with that mode and are called animals. Phylads which adopted or later switched to the chylotropic mode of nutrition are referred to the plant or the animal kingdom according to their other characteristics and probable evolutionary relationships.

Above the level of the bacteria, all autotrophic organisms (so far as known) contain chlorophyll-a, which is usually the principal photosynthetic pigment (Rabinowitch, 1954). The other chlorophylls and the accessory pigments vary from group to group, but the presence of chlorophyll-a is apparently constant. Loss of chlorophyll has occurred repeatedly. Among the unicellular flagellates, which have not proceeded very far in the direction of plant evolution, the loss of chlorophyll has repeatedly led to a holozoic mode of nutrition, with further evolution proceeding along animal, instead of plant, lines. Above the flagellate level, loss of chlorophyll has led only to chylotrophic nutrition, the phylads being so committed to evolution along plant lines that they are no longer able to develop the characters needed for holozoic nutrition. Such well known green plants as *Utricularia, Drosera, Dionaea* and *Sarracenia* have undergone some evolutionary modification toward a holozoic mode of nutrition, but they are still obviously plants.

There is no evidence that the acquisition of chlorophyll has occurred more than once, and it is possible to make a consistent scheme on the premise that this single acquisition occurred at the bacterial level. A premise of dual or multiple origin of chlorophyll, on the contrary, poses insuperable difficulties to the development of a satisfactory phyletic scheme; I believe this will become obvious to the reader in the following pages.

Evidence which has been obtained by observations with the electron microscope, chiefly within the past decade, shows that the flagella and cilia of all groups (except bacteria) which have these organelles are of the same basic structure: a core of two (rarely only one) strands surrounded by a sheath of usually nine strands which are chemically different from the strands of the core. This has been dem-

[1]"Chylotrophic" is here introduced as a new word describing organisms which characteristically absorb organic food in solution instead of making or ingesting it. All saprobes and many parasites are chylotrophic.

onstrated for such widely divergent kinds of organisms as unicellular flagellates (of many sorts), green algae (unicellular and multicellular forms), brown algae, Phycomycetes, mosses, ferns, *Paramoecium*, molluscs, fish, frogs, cattle, sheep and man. (Manton, 1952; Manton, Clarke and Greenwood, 1953).

The flagella of bacteria, in contrast to those of higher organisms, generally consist of single strands. Sometimes several flagella are very closely placed and act as a single organelle, but anatomically they retain their individual identity (Stocker, 1956). This latter condition may suggest the evolutionary origin of the more complex type of flagellum, which does not exist (or at least is not yet known) among the bacteria.

Recent studies show an apparent homology between typical flagella and certain other cell organelles, notably centrioles, which also have a nine-strand periphery, although without the two-strand central core. (Ehret, 1960; Inoué, 1959; Roth, 1959). The central strands are also generally lacking from the basal granule (blepharoplast) of a flagellum. It remains to be determined whether flagella may be extruded centrioles, or centrioles may be wandering blepharoplasts, or just what, but for our purposes the essential fact is the basic similarity of flagella in different kinds of organisms, except the bacteria.

No survival value has been suggested for the two- plus nine-strand structure of flagella, as compared to any other possible compound structure, nor is there any obvious reason why this pattern is mechanically easier than some other pattern or patterns. The evidence from flagellar structure, therefore, suggests a common evolutionary origin, above the level of bacteria, of all other organisms which have flagella or cilia at any stage in the life cycle. The angiosperms, which lack these structures entirely, are generally conceded to be related to, and eventually derived from, the more primitive vascular plants, which do have ciliate sperms. The blue-green algae and the red algae, which lack flagella, are tied to the other chlorophyllous organisms by the common possesion of chlorophyll-a as well as by some other features mentioned later in this paper. It therefore appears that all organisms above bacteria have a common origin just above the bacterial level. The status of the bacteria as ancestral to all the other groups is discussed later in this paper.

In terms of evolution, the holozoic mode of nutrition was first achieved among the unicellular flagellates. The theory developed in this paper indicates that the possession of chlorophyll and a cell wall

is primitive among the unicellular flagellates, and that the absence of these is derived. Loss of chlorophyll has evidently occurred independently in several groups, sometimes associated with the assumption of a holozoic mode of nutrition. Some of the chrysomonads and dinoflagellates ingest food particles directly, as well as being photosynthetic (Smith, 1955, pp. 157, 171). Loss of chlorophyll and the assumption of a completely holozoic mode of nutrition would seem to be an easy evolutionary step for such organisms.

Among the protozoa the flagellates are considered by Hyman (1940) and others to be ancestral to the non-flagellated forms, and among the flagellates the groups with some chlorophyllous members are regarded as more primitive than the wholly non-chlorophyllous groups. These views are readily compatible with the view here presented that the protozoa were derived from several groups of unicellular flagellates by loss of chlorophyll and subsequent evolution along holozoic lines. The various groups of metazoa were, of course, derived eventually from the protozoa.

Each of the major groups of chlorophyllous flagellates has one or more members or immediate derivatives in which the vegetative body is multicellular or colonial, with definite cell walls and without flagella. "Thus, with the possible exception of the chloromonads, all the various groups (orders) of flagellates which protozoologists place in the subclass Phytomastigina of the class Mastigophora are phylogenetically connected to organisms of truly algal nature" (Smith, 1950). Exclusion of any of the chlorophyllous flagellates from the plant kingdom is, therefore, seriously prejudicial to the scheme of classification.

The fungi and the chylotrophic bacteria are the only large groups of chylotrophic organisms which do not clearly relate to unquestioned plants or unquestioned animals (in the two-kingdom system). The bacteria also include many autotrophic organisms, both photosynthetic and chemosynthetic, and no holozoic ones. It is, therefore, customary, convenient and proper to refer the whole group to the plant kingdom. The bulk of the fungi resemble typical plants in being non-motile, in the production of spores, and in having definite walls. It is therefore customary to refer this group also to the plant kingdom; common sense tells us that, as between plants and animals, a mushroom must be associated with plants. The more or less holozoic nutrition of the Myxomycetes is an embarrassment to this disposal of the fungi, but the mycologists have learned to live with this problem and the rest

of us will have to do the same. The fungi could be detached from the plant kingdom, however, without any serious effect on the rest of the system, and in any scheme which recognizes more than two kingdoms of organisms the claim of the fungi to status as a separate kingdom merits consideration. The case for a three-kingdom system, with the fungi as the third kingdom, has been summarized by Rogers (1948).

The evolutionary origin and proper taxonomic status of the viruses remain to be clarified. Some or all of them may prove to be derived from bacteria by progressive simplification; some of them may be protoplasmic organelles which have escaped from the control of the protoplasmic system that brought them into being (Luria, 1953). So far as is now known, all true viruses reproduce, or are reproduced, by organization of particles de novo in the protoplasm of the host; the viral components enter into the metabolic system of the host cell and subvert the system into producing more virus particles. This method of reproduction is so different from the fission of bacteria, as well as from the cell division of other organisms, that the viruses would have to be treated as a separate (and perhaps polyphyletic) division if they were included in the plant kingdom. The name "Virophyta Rothm." (1951) is available if anyone wishes to use it. In any case, inclusion or exclusion of the viruses does not affect the rest of the system, and no further attention is paid to them in this paper.

In the light of the foregoing considerations, I believe that a coherent classification of the plant kingdom requires the inclusion of all autotrophic organisms, plus the chylotrophic bacteria and such other non-chlorophyllous organisms as are clearly related to plants and not to animals. The fungi are also included in preference to making a third kingdom for them; they surely do not go with the animals. For the purposes of this paper there is no need to draw a precise line among the flagellates as to which of the colorless forms should be included and which should be excluded, so long as it is realized that the characteristics of the flagellated taxa here recognized are based primarily on the chlorophyllous members. If the protozoologists continue to feel that a coherent classification of the protozoa requires inclusion of the chlorophyllous flagellates, the dual position of these organisms will merely have to be accepted. The evidence is clear that the whole animal kingdom and the bulk of the plant kingdom are descended from such organisms.

THE SUBKINGDOMS

The plant kingdom is here treated as consisting of two subkingdoms, the Embryophyta (Cormophyta) and the Thallophyta. The familiar name Embryophyta, which was first formally used in the status of a subkingdom by Tippo (1942), is adopted in preference to the older name, Cormophyta (Endlicher, 1836), because the latter name is etymologically misleading and has often been used in a more restricted sense to apply only to the vascular plants or to some part of them. The Embryophyta are a very well marked natural group ultimately derived from the green algae (one of the groups of Thallophyta), as indicated inter alia by the pigmentation, food reserves, cell walls and detailed structure of the flagella. The Thallophyta are a very diverse group but still a natural one in the sense that the bacteria are a common ancestor to the other members of the group and that the inter-relationships among the members of the Thallophyta do not involve the Embryophyta. The presumed relationships of the divisions and classes of plants are indicated in the accompanying chart. A synoptical key to the groups is presented after a necessary diversion regarding proper termination of the names of classes.

ENDINGS OF NAMES OF CLASSES

The Stockholm (1952) version of the International Code of Botanical Nomenclature unexpectedly blossomed forth with a new recommendation that classes of the Cormophyta bear the uniform termination "opsida," and this recommendation has been continued without change in the current edition of the rules. The disappearance of the old Article 32 from the Paris (1956) version of the rules does not diminish the cogency of the deleted article, and perhaps does not indicate a disrespect for its principle, but in any case the new recommendation is not one that I am disposed to accept.

The ending -opsida was first used in 1899, when Jeffrey proposed to divide all vascular plants on anatomical grounds into two groups, the Pteropsida and Lycopsida. It soon became evident that the Lycopsida sensu Jeffrey were a heterogeneous group, and the Sphenopsida (Scott, 1909) and Psilopsida (Eames, 1936) were successfully re-

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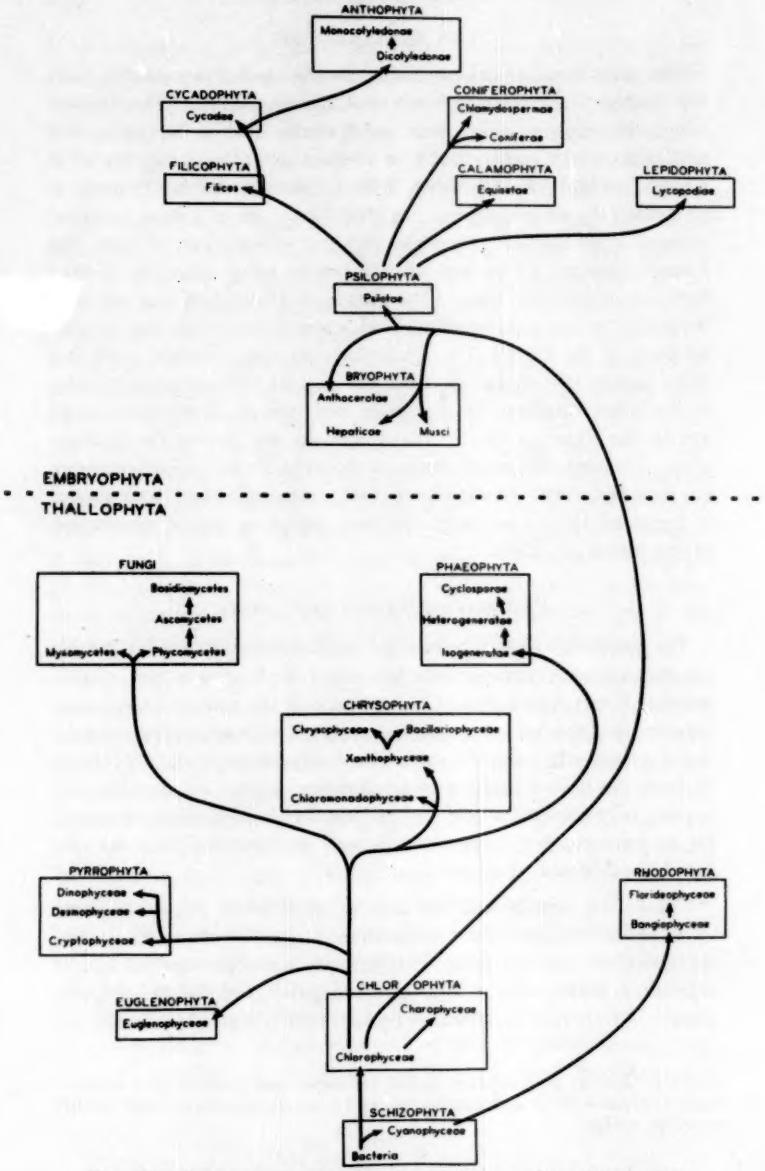
2 "The Code of nomenclature should be simple and founded on considerations sufficiently clear and forcible for every one to comprehend and be disposed to accept."



The Divisions and Classes of Plants as Proposed in this Article

moved as the Lycopsida were progressively restricted. It is now becoming increasingly evident that the Pteropsida are also heterogeneous, inasmuch as the Coniferophyta do not properly belong with the other members of the group. Lam (1948a) proposed to restrict the name Pteropsida to the ferns and pteridosperms alone.

The names Lycopsida, Psilopsida, Pteropsida and Sphenopsida are still the only "-opsida" names that have any general botanical currency, although Lam proposed some others in 1948, and still others have recently been proposed (e.g., Boivin, 1956) in accordance with the new recommendation which Lam sponsored at the 1950 Congress. The taxonomic rank of the names bearing these endings, has varied with different authors. Jeffrey (1899, 1902), who proposed the first two, did not indicate their taxonomic status; he called them "groups" or "stocks." Scott, who was the first to use "-opsida" names in a formal taxonomic sense (1909), and who himself created one of them, considered them to represent divisions. Zimmerman (1930) likewise called them divisions. Eames (1936), who proposed the fourth name, is vague about their rank; from his discussion they could be divisions, subdivisions or classes, although I think that the best inference, if any inference is to be drawn at all, is that they represent divisions. Tippo (1942) used them for subphyla (equivalent to subdivisions), and this usage has recently been accepted in a number of American textbooks. So far as I am aware, Lam (1948a) was the first to use these names formally to indicate classes, and it was largely due to his efforts that a recommendation (though not an article, as he at first proposed) supporting this usage was accepted at the Stockholm Congress in 1950.

It seems quite likely that morphologists will wish to continue to use the term Pteropsida for plants with megaphylls and/or leaf-gaps, even though it is now clear that the Coniferophyta are not directly related to the remainder of the Pteropsida, and regardless of whether or not taxonomists wish to limit application of this name to the ferns alone. They will also wish to continue to refer to the Psilopsida, Lycopsida and Sphenopsida, regardless of the taxonomic rank which may be assigned to these groups. The morphologists do, after all, have prior claim to the use of this ending, and priority has been considered to be one of the guiding principles of taxonomic nomenclature.

I very much doubt that uniformity of endings for class names is worth the effort and confusion that would be necessary to uproot and

replace such familiar names as Hepaticae and Musci, to mention only two. In any case, the "-opsida" ending will not adequately serve the purpose; instead it tends to "cause error or ambiguity or throw science into confusion" (Preamble to the 1956 edition of the Rules).

Probably the most familiar class endings among the embroyphytes are "-ae" (Hepaticae, Anthocerotae, Coniferae, etc.), "eae" "Monocotyledoneae, Dicotyledoneae, etc.), and "-inae" (Filicinae, Equisetinae, Lycopodinae, etc.). In the current edition of the rules, the "-eae" ending has been reserved for tribes, and the "-inae" ending for subtribes, and both of these usages have some prior acceptance. Therefore, only the "-ae" ending remains available as a standard for classes, and I have changed some existing "-eae" and "-inae" endings to "-ae." It seems unnecessary to modify the familiar name Musci, and the form "Filices" is a well established alternative to the now unacceptable "Filicinae."

SYNOPSIS OF THE DIVISIONS AND CLASSES OF PLANTS

1 Gametangia and sporangia, when present, generally unicellular, or sometimes multicellular with all cells fertile (gametangia multicellular and with a sterile jacket in Charophyceae, but then anatomically very different from those of the Embryophyta); zygotes (except in many Rhodophyta and a few Phaeophyta) not developing into multicellular embryos while still attached to the parent gametophyte; plants without xylem, and ordinarily without phloem.

Subkingdom I. THALLOPHYTA.

2 Nucleus, if present, relatively simple in structure, lacking a nucleolus and ordinarily lacking a nuclear membrane, apparently not dividing mitotically; plants mostly asexual, or with parasexual processes which apparently do not involve nuclear fusion and meiosis; plastids, central vacuoles, and contractile vacuoles wanting; principal food reserves generally polysaccharides which resemble glycogen.

Division 1. SCHIZOPHYTA.

3 Plants mostly without chlorophyll and not photosynthetic; photosynthetic forms have bacteriochlorophyll instead of chlorophyll-a, and do not produce oxygen as a result of photosynthesis; carotenoid pigments do not include myxoxanthin

and myxoxanthophyll; no phycobilin pigments; cell wall mostly nitrogenous, seldom with cellulose

Class Bacteria.

3 Plants mostly with chlorophyll, photosynthetic and producing oxygen as a result; chlorophyll is chlorophyll-a; carotenoid pigments include myxoxanthin and myxoxanthophyll, unique to this group; one or two phycobilin pigments (typically phycocyanin) always associated with the chlorophyll; cell wall of polysaccharides, including some cellulose

Class Cyanophyceae.

2 Nucleus highly organized and complex, with chromonemata, nucleolus, and nuclear membrane, and ordinarily dividing mitotically; plants often sexual, with nuclear fusion and meiosis; photosynthetic pigments, when present, generally borne in plastids; protoplast (except in the Bangiophyceae) usually with either a central vacuole or one or more contractile vacuoles; food reserves diverse

4 Chlorophyll usually present and the plants photosynthetic (lacking chiefly among some of the unicellular flagellates); cell walls ordinarily not chitinous, mostly of polysaccharides, often including cellulose, sometimes siliceous, or wanting and the cell then bounded by a flexible, living membrane.

5 Plants with one or two phycobilin pigments, including phycoerythrin, nearly always multicellular at maturity, not producing flagellated cells of any sort; principal food reserve usually floridean starch, a glycogen-like polysaccharide; chiefly marine plants

Division 2. RHODOPHYTA.

6 Cells of the thallus without pit-connections; cell divisions generally intercalary within the thallus; no gonimoblast filaments produced, the zygote dividing directly and probably meiotically to form either carpospores or cells which immediately give rise to carpospores by subsequent mitotic divisions; cells usually with a single chloroplast and without a central vacuole

Class Bangiophyceae.

6 Cells of the thallus with prominent pit-connections; thallus of basically filamentous construction (filaments often

compacted), and cell division commonly more or less restricted to the apical cells of the filaments; carpospores formed on gonimoblast filaments, the first division of the zygote (except in some Nemalionales) generally being mitotic; cells usually with a central vacuole and often with several or many chloroplasts

Class Florideophyceae

5 Plants (except some Cryptophyceae) without phycobilin pigments; food reserves diverse, but not of floridean starch, and generally not glycogen-like; plants often with flagellated cells at some stage of the life cycle

7 Chloroplasts grass-green, the associated pigments masked by the chlorophyll; chlorophyll of a and b types only; flagella, when present and more than one, generally all alike.

8 Cells without a gullet; plants unicellular, colonial, or multicellular, usually with cell walls, with or without flagella, the flagella when present at least usually of the whiplash type; food reserves typically starch; often sexual, sometimes asexual

Division 3. CHLOROPHYTA.

9 Gametangia not surrounded by sterile jackets; thallus simple or more or less complex, but not like that of the Charophyceae.

Class Chlorophyceae.

9 Gametangia surrounded by sterile jackets; thallus relatively complex, consisting in part of an erect, multicellular axis with whorled branches.

Class Charophyceae.

8 Cells with a gullet, usually solitary and flagellated, mostly naked, occasionally loricate, seldom with a definite wall; flagella pectinate; food reserves typically paramylum, a starch-like carbohydrate; asexual

Division 4. EUGLENOPHYTA.
(Class Euglenophyceae)

7 Chloroplasts mostly yellowish green to brownish, the chlorophyll more or less masked by the associated carotenoid pigments; chlorophyll-b wanting, but chloro-

phyll-c or -e often present; flagella, when present, mostly 2-several and dissimilar, typically one whiplash and one tinsel (pectinate or pinnate)

10 Plants unicellular to colonial or sometimes filamentous, most of the filamentous forms lacking fucoxanthin; food reserves diverse, but not laminarin

11 Cell walls, when present, usually composed of cellulose, sometimes organized into 2 valves, but not silicified; food reserves mostly starch or starch-like substances, sometimes oils; most asexual, unicellular flagellates, seldom colonial or filamentous; one or both flagella often pectinate; carotenoid pigments peridinin, dinoxanthin, and neodinoxanthin typically present (perhaps not in the Cryptophyceae)

Division 5. PYRROPHYTA.

12 Chromonemeta not moniliform; cells mostly naked, often with a gullet; flagella only slightly dissimilar, at least sometimes both pectinate; phycobilin pigments sometimes present

Class Cryptophyceae

12 Chromonemata moniliform; cells with or without a cell wall, but without a gullet; flagella distinctly dissimilar, one often or always whiplash, the other at least frequently pectinate; phycobilin pigments wanting

13 Motile cells with two apically inserted flagella, without a grove; cell wall, when present, of two longitudinal valves which are not divided into definitely arranged plates

Class Desmophyceae

13 Motile cells with a transverse or spiral groove in which two flagella are attached; one lying in the groove and encircling the cell, the other trailing; cells naked or more often with a cellulose wall, this often of interlocking plates which are seldom organized into two longitudinal valves.

Class Dinophyceae

11 Cell walls, when present, seldom containing appreciable quantities of cellulose, often silicified, very often of two valves; food reserves leucosin (a polysaccharide) and/or oils; plants typically unicellular or loosely colonial, sometimes (especially in the Xanthophyceae) filamentous or even coenocytic; often produce statospores, unique to this division; flagella, when present, generally two and dissimilar, one whiplash, the other pinnate; carotenoid pigments do not include peridinin, dinoxanthin, or neodinoxanthin

Division 6. CHRYSOPHYTA.

14 Chloroplasts mostly yellowish green (or green in some Chloromonadophyceae); fucoxanthin wanting; plants sometimes with chlorophyll-e, unique to this group; cell wall, when present, usually not highly silicified

15 Plants unicellular flagellates without cell walls

Class Chloromonadophyceae.

15 Plants usually with cell walls, the vegetative cells seldom flagellated; vegetative cells, when without a wall, with or without flagella

Class Xanthophyceae.

14 Chloroplasts golden brown; plants with fucoxanthin and without chlorophyll-e

16 Cells mostly flagellated or amoeboid and bounded by a flexible living membrane which may bear siliceous scales, often also loricate, seldom with a definite wall, and this not highly silicified when present; plants lacking chlorophyll-c and ε-carotene

Class Chrysophyceae.

16 Cells bounded by a highly silicified wall composed of two overlapping halves, not flagellated (except some of the gametes); mostly sexual, the vegetative cells apparently always diploid; plants with chlorophyll-c and ε-carotene

Class Bacillariophyceae.

10 Plants filamentous or more complex, non-motile, with brownish chloroplasts that contain fucoxanthin and other pigments; chiefly marine, usually sexual; food reserves commonly laminarin, a soluble, dextrin-like polysaccharide; cell wall contains cellulose

Division 7. PHAEOPHYTA.

17 Plants with well developed alternation of generations, both the sporophyte and the gametophyte multicellular

18 Sporophyte and gametophyte similar

Class Isogeneratae.

18 Sporophyte and gametophyte dissimilar, the sporophyte always the larger

Class Heterogeneratae.

17 Plants with only the sporophyte generation multicellular; haploid stage represented by the "spores" which function directly as gametes

Class Cyclosporae.

4 Chlorophyll wanting and plants not photosynthetic; cell walls (or limiting membrane) usually chitinous (cellulose among some of the Phycomycetes, of unknown chemical composition among the Myxomycetes)

Division 8. FUNGI

19 Plants plasmodial and generally capable of ingesting food as well as absorbing it; flagellated cells, when produced, generally bearing 2 unequal whiplash flagella; spores usually numerous in a sporangium

Subdivision Myxomycotina.
Class Myxomycetes.

19 Plants consisting of filaments or cells that are usually bounded by definite walls, obtaining food by absorption only; flagellated cells, when produced, with one or two flagella, the biflagellated forms always with one whiplash and one tinsel (usually pinnate) flagellum

Subdivision Eumycotina.

20 Filaments coenocytic or occasionally with scattered septa, or the plants unicellular; perfect stage usually consisting of a zygospore or an oospore, not borne on a defin-

ite fruiting body; flagellated cells often produced; spores (either sexual or asexual) often numerous in a sporangium

Class Phycomycetes.

20 Filaments generally septate, or the plants unicellular; perfect stage usually of one or more asci or basidia that are often borne on a definite fruiting body; flagellated cells never produced; sexual spores usually few and definite in number; asexual spores never enclosed in a sporangium

21 Sexual spores borne within a sporangium (the ascus), typically 8, seldom 4, occasionally 16, or more; filaments without clamp connections

Class Ascomycetes.

21 Sexual spores borne externally on a basidium, typically 4, or the basidium sometimes failing to produce spores; filaments often with clamp connections

Class Basidiomycetes.

1 Gametangia and sporangia multicellular, the outermost cells forming a sterile jacket, or the gametangia reduced and scarcely developed in some plants that usually have xylem and phloem; zygote ordinarily developing into a multicellular embryo while still attached to the parent plant

Subkingdom II. EMBRYOPHYTA.

22 Plants without xylem and phloem; sporophyte partially or wholly parasitic on the gametophyte, not becoming independent

Division 9. BRYOPHYTA.

23 Sporophyte with a meristematic region near the base; archegonia and antheridia originating from internal cells of the thallose, dorsiventral gametophyte; chloroplasts with pyrenoids; sporophytes with stomates, and usually with a columella in the capsule

Class Anthocerotae.

23 Sporophyte without a meristematic region; antheridia and archegonia originating from superficial cells; chloroplasts without pyrenoids

24 Gametophyte usually dorsiventral, without a distinct pro-

tonemal stage; capsule without a columella but usually with elaters; rhizoids unicellular; stomates wanting
Class Hepaticae.

24 Gametophyte with a filamentous or dorsiventral and thallose protonemal stage, followed by the development of gametophores with phyllidia spirally and symmetrically arranged around a caulidium; capsule without elaters but usually with a columella; rhizoids multicellular; sporophyte often with stomates Class Musci.

22 Plants ordinarily with xylem and phloem; sporophyte physiologically independent of the gametophyte at maturity (Tracheophyta)

25 Central cylinder without leaf-gaps; leaves of modern forms always uninerved or nerveless microphylls; modern forms not producing seeds, both generations physiologically independent of each other at maturity

26 Plants without true roots, the subterranean portion lacking root caps and anatomically not much different from the aerial stem; branching chiefly dichotomous
Division 10. PSILOPHYTA (Class Psilotae).

26 Plants with true roots that have root caps and are anatomically well differentiated from the stem; branching dichotomous to sympodial or monopodial

27 Leaves mostly alternate or opposite; stem not jointed, sporangia axillary (or on the adaxial surface near the base) to vegetative or more or less modified leaves that may or may not be aggregated into a terminal strobilus
Division 11. LEPIDOPHYTA (Class Lycopodiae).

27 Leaves whorled; stem joined; sporangia borne on highly modified sporangiophores that are aggregated into a characteristic terminal strobilus
Division 12. CALAMOPHYTA (Class Equisetae).

25 Central cylinder usually with leaf-gaps; leaves (many conifers excepted) usually magaphylls with a branching vein system (Pteropsida)

28 Plants not producing seeds, both generations physiologically independent at maturity

Division 13. FILICOPHYTA (Class Filices)

28 Plants producing seeds, the gametophyte never becoming physiologically independent, the young sporophyte as well as the female gametophyte usually retained on the old sporophyte for some time (Spermatophyta)

29 Ovules naked, not enclosed in an ovary; female gametophyte multicellular, composed of 500 or more cells, and (except in a few coniferophytes) producing definite archegonia; wood lacking vessels, except in the Chlamydospermae; food reserves of the seed largely stored in the body of the female gametophyte; no triple-fusion cell (Gymnospermae)

30 Leaves simple and mostly relatively small (dichotomously branched in some fossil forms), mostly not at all fern-like; plants with more or less well developed secondary growth, and usually with branching stems; modern members (*Ginkgo* excepted) with naked sperms

Division 14. CONIFEROPHYTA.

31 Male cones simple; female cones simple to compound or scarcely developed; ovules with 1 integument, this usually not forming a very long micropylar tube; vessels wanting; leaves seldom opposite; embryo usually with more than 2 cotyledons; resin canals very often present

Class Coniferae.

31 Male and female cones compound; ovules with 2 integuments, at least the inner integument forming a very long micropylar tube; secondary wood with vessels; leaves opposite; embryo with 2 cotyledons; resin canals wanting

Class Chlamydospermae

30 Leaves usually (including all the living species) pinnately compound, typically large and more or less fern-like; plants with relatively little or no secondary

growth, and with the stem seldom much branched; modern members with ciliate sperms
Division 15. CYCADOPHYTA (Class Cycadae).

29 Ovules enclosed in an ovary; female gametophyte of a few (typically 8) cells (or a similar free-nuclear protoplast), not producing archegonia; vessels usually present; fertilization accompanied by the formation of a triple-fusion cell, which typically gives rise to the food storage tissue of the seed
Division 16. ANTHOPHYTA.

32 Embryo mostly with two cotyledons; plants usually with an evident fascicular cambium; vascular bundles in herbaceous forms usually borne in a ring which encloses a pith; floral parts, when of definite number, typically borne in sets of 5, less often 4, seldom 3; leaves mostly pinnately or palmately veined; pollen mostly of tricolpate or tricolpate-derived type
Class Dicotyledonae.

32 Embryo with one cotyledon; plants without fascicular cambium, and usually without any sort of cambium; vascular bundles generally in more than one ring, or scattered; floral parts, when of definite number, typically borne in sets of 3, seldom 4, never 5; leaves mostly parallel-veined; pollen mostly of monocolpate or monocolpate-derived (not tricolpate) type
Class Monocotyledonae.

OUTLINE OF THE CLASSIFICATION OF THE PLANT KINGDOM

In the following skeleton outline of the foregoing classification, I deliberately follow the customary practice of giving the names of higher groups without citations. Names above the rank of order are now exempted from the principles of priority and typification under the rules of nomenclature, as they have always been in actual botanical practice. The listing of authors and places and dates of publication, therefore, tends to become superfluous. The exemption from priority also tends to vitiate the still technically effective requirements regarding validity of publication, especially the Latin diagnosis rule. I shall,

however, follow the rules on the few new names proposed in this paper.

I. Subkingdom THALLOPHYTA.
1. Division Schizophyta.
1a. Class Bacteria (Schizomycetes).
1b. Class Cyanophyceae.
2. Division Rhodophyta.
2a. Class Bangiophyceae.
2b. Class Florideophyceae (Florideae sens. strict; Subclass Florideae Schmitz in Engl. Syll. Vorles. spec. & med-pharm. Bot. Berlin, 1892. p. 16).
3. Division Chlorophyta.
3a. Class Chlorophyceae
3b. Class Charophyceae.
4. Division Euglenophyta.
4a. Class Euglenophyceae.
5. Division Pyrrophyta.
5a. Class Cryptophyceae.
5b. Class Desmophyceae.
5c. Class Dinophyceae.
6. Division Chrysophyta.
6a. Class Chloromonadophyceae.
6b. Class Xanthophyceae. (Heterokontae).
6c. Class Chrysophyceae.
6d. Class Bacillariophyceae. (Diatomeae).
7. Division Phaeophyta.
7a. Class Isogeneratae.
7b. Class Heterogeneratae.
7c. Class Cyclosporae.
8. Division Fungi. (Class Fungi Endlicher, Gen. Pl. 1: ii. 1836.)
Subdivision Myxomycotina. (Suborder Myxogastres Fries, Syst. Myc. 3:67. 1829)
8a. Class Myxomycetes.
Subdivision Eumycotina. (Pilze, Sensu DeBary, Vergl. Morph. & Biol. der Pilze, Mycetozoen, and Bacterien. 1884).
8b. Class Phycomycetes (incl. Archimycetes).
8c. Class Ascomycetes.
8d. Class Basidiomycetes.

II. Subkingdom EMBRYOPHYTA (Cormophyta Endl., sens. lat.).
9. Division Bryophyta.

9a. Class Anthocerotae.
9b. Class Hepaticae.
9c. Class Musci.
10. Division Psilophyta (Psilopsida).
10a. Class Psilotae (Class Psilotales Engler & Gilg, Syllabus, 8th ed., p. 101. 1912)
11. Division Lepidophyta (Lycopsida, sens. strict.).
11a. Class Lycopodiae (Class Lycopodinae Eichl. Syllabus, ed. 2, p. 16, 1880)
12. Division Calamophyta (Sphenopsida).
12a. Class Equisetae (Class Equisetinae Eichler, Syllabus, ed. 2, p. 16. 1880).
13. Division Filicophyta (Class Filicinae Eichler, Syllabus, ed. 2, p. 17. 1880).
13a. Class Filices.
14. Division Cycadophyta.
14a. Class Cycadae.
15. Division Coniferophyta.
15a. Class Coniferae (Incl. Ginkgoales, Taxales, Cordaitales).
15b. Class Chlamydospermae (Gnetales, sens. lat.).
16. Division Anthophyta.
16a. Class Dicotyledonae.
16b. Class Monocotyledonae.

DISCUSSION

BACTERIA

The bacteria give every indication of being the most primitive group of living organisms, from which all other kinds of organisms are eventually descended. The origin of the bacteria themselves is obscure.

Modern speculations about the origin of life usually center around the theory promulgated by Oparin (1938, 1957). According to this line of thought, organic matter was first formed by happenstance chemical reactions promoted by ultra-violet light and taking place in the as yet fresh (not salty) water of the sea. Evidence from non-biological sources tends to confirm Oparin's argument that the primitive atmosphere of the earth contained little, if any, free oxygen (Urey, 1952), and experimental studies support the belief that amino acids

and other organic compounds would be formed under the conditions thought to have existed at that time (Miller, 1953; Paschke, Chang, and Young, 1957).

It is believed that the organic molecules very gradually accumulated and that reactions among them led to the formation of larger molecues. Electro-chemical attractions might reasonably be expected to hold some of these molecules together as colloidal particles. When such an aggregation came to include the proper chemical compounds to promote the formation of additional such compounds, the first organism came into being. Increase in the number of such primitive organisms may have occurred simply by the failure of the mass to hold together as its volume increased.

Under this concept, the first organisms were heterotrophic. As more and more of the previously formed organic molecules became incorporated into the molecule-systems which represented the first organisms, a premium must have been placed on the ability to use less and less complex substances as raw materials, and finally on the ability to tap some new source of energy. If the atmosphere at that time contained relatively little free oxygen, these organisms were anaerobic. Any new source of energy, therefore, probably would not involve free oxygen, and thus would not resemble the chemosynthetic processes now carried out by the iron and sulfur bacteria. Free oxygen is used in these latter processes. The first new source of energy may possibly have been photosynthesis resembling that of some modern bacteria, in which organic compounds are used as hydrogen-donors, and free oxygen is neither used nor released. Photosynthesis in which water serves as the hydrogen-donor, and oxygen is released, would under such a hypothesis be a later development.

Aerobic organisms characteristically contain the cytochrome system of respiratory enzymes, which are chemically related to chlorophyll. Anaerobic organisms generally do not have the cytochrome system. According to the most widely accepted current hypothesis, it was not until a considerable supply of atmospheric oxygen had been built up by the newer type of photosynthesis that the cytochrome system, which uses free oxygen, was developed by modification of chlorophyll or of its chemical precursors. Under such a hypothesis, all aerobic organisms, including the aerobic bacteria, would be derived eventually from photosynthetic anaerobes more or less similar to some of the present day

photosynthetic bacteria. A summary of this general line of thought is presented by Thimann (1955).

Most students of bacterial cytology, for example, Robinow (1956) and Bisset (1956), are now convinced that bacteria characteristically have one or more DNA-containing bodies which function as nuclei but which do not have the complex organization of the nucleus of higher organisms. The development of chlorophyll, the cytochrome system, and a primitive nucleus thus all occurred within the bacteria.

The present day photosynthetic bacteria do not produce oxygen in photosynthesis. We can only speculate as to whether the development of oxygen-releasing photosynthesis was directly correlated with the evolution of chlorophyll-a and β-carotene. In any case these two pigments are unknown in bacteria and are characteristic of all other photosynthetic groups, and oxygen is a normal by-product of photosynthesis among all photosynthetic organisms except bacteria. Most of these organisms also contain additional chlorophylls and additional carotenoid pigments, but chlorophyll-a is normally the principal chlorophyll, and β-carotene the principal carotene.

BLUE-GREEN ALGAE

The blue-green algae (Cyanophyceae) diverged from the main line of photosynthetic organisms before a highly organized nucleus had been developed. The accessory photosynthetic pigments of the Cyanophyceae always include one or two phycobilins, which are otherwise known only among the red algae (Rhodophyta) and some of the cryptomonads (Cryptophyceae). Phycobilin pigments (phycocyanin and phycoerythrin) are water-soluble proteinaceous compounds, quite unlike the carotenoid pigments and chlorophyll, which are fat-soluble.

The blue-green algae are evidently derived from the bacteria. Both have a primitive type of nucleus, different from that of nearly all other organisms. Neither group has been demonstrated to have typical sexual processes, although parasexual processes are known in some of the bacteria. Bacterial starch and cyanophycean starch, the characteristic food reserves, are chemically similar, both resembling glycogen. Both groups usually have the cells enclosed in a gelatinous sheath, although similar sheaths occur among some of the other algae as well. Certain blue-green algae and certain bacteria differ from nearly all other organisms in being able to reduce atmospheric nitrogen. Certain bacteria and certain blue-green algae thrive at temperatures far higher than can

be withstood by ordinary cells of other organisms. Some of the chemosynthetic bacteria are so similar in appearance to some of the blue-green algae that some students have suggested that the organisms in question are more closely related to the Chyanophyeae than to the Bacteria. *Beggiatoa,* in particular, is morphologically very similar to *Oscillatoria* of the blue-green algae, and the filaments wave back and forth in similar fashion. Yet *Beggiatoa* and its immediate relatives resemble some undoubted bacteria, and differ from the blue-green algae, in oxidizing sulfur as a source of energy for the manufacture of food.

Copeland (1956) has gone so far as to transfer all of the chlorophyllous bacteria and most of the chemo-autotrophic ones to the same class as the blue-green algae, but this carries its own problems and does not sharpen the distinction between the two groups. The iron bacterium *Sphaerotilus* produces reproductive cells with flagella of the bacterial type (Stocker, 1956; Stokes, 1954), whereas flagellated cells are wholly unknown in the Cyanophyceae proper, with which Copeland would put this genus. Moreover, some of the photosynthetic bacteria are facultatively saprobic, losing their chlorophyll in the absence of light; under such circumstances they do not differ significantly from other bacteria in general.

Algologists often treat the blue-green algae as a separate division, Cyanophyta, instead of grouping them with the bacteria into a division Schizophyta. Such a treatment obscures the relationship between the two groups and tends to defeat the purposes of classification. There is no need for single-class divisions in this instance.

It has sometimes been casually suggested that the simple structure of the bacteria and blue-green algae is due to reduction from more complex ancestors. The evidence is all to the contrary. Reduction is a well-known force in organic evolution, but it can scarcely be expected, for instance, to produce single strand flagella from multi-strand ones of the type found in all other flagellated organisms. On the basis of comparative morphology and physiology, the bacteria stand unshakably at the base of the evolutionary tree, with the blue-green algae as slightly more advanced near relatives. If any further evidence is desired, it is provided by the fossil record, which, so far as it can be deciphered, carries both of these groups of organisms well into pre-Cambrian time (Gruner, 1925; Walcott, 1914; Tyler and Barghoorn, 1954).

A few genera of blue-green algae are known only in symbiotic association with colorless algae of other types, in effect acting as chloro-

plasts for the cells in which they are enclosed. A brief discussion of the situation, with references to the original literature, is given by Smith (1950). Skuja (1948, 1953) has recently proposed that the organisms involved in these associations be distinguished as a separate division, Glaucophyta, with a single class Glaucophyceae. I see no need or justification for this segregation. The blue-green algae in these associations are not essentially different from other blue-green algae, and at least one of them, *Cyanoptyche,* can live and divide independently of the host. The host cells, whatever they are, have nothing to do with the blue-green algae taxonomically. They have been thought to be modified members of the Chlorophyceae, but Skuja points out that the zoospores of *Gloeochaete* have two dissimilar flagella instead of the similar flagella that would be expected in a member of the green algae. The Glaucophyta have no more claim to separate taxonomic status than the lichens.

RED ALGAE

The Rhodophyta (red algae) are so different from all other algae as to be taxonomically rather isolated; their only likely relatives are the blue-green algae. The red algae and blue-green algae are alike in having phycobilin pigments, which are not known in other organisms except certain Cryptophyceae. They are also similar in the complete absence of flagellated cells. Furthermore, floridean starch, the characteristic carbohydrate reserve of the red algae, is chemically allied to cyanophycean starch, the characteristic carbohydrate reserve of the blue-green algae; both of these compounds are similar to glycogen and the amylopectin fraction of ordinary starch.

The red algae differ from the blue-green algae in the presence of a vesicular nucleus, in having definite plastids, in having chlorophyll-d in addition to chlorophyll-a, in the usually more complex structure of the thallus, and in being usually sexual, often with a very complex life cycle. All of these features may be regarded as evolutionary advances over the condition in the blue-green algae. The sexual processes in the red algae are so different from the sexual processes of other algae that a separate origin of sexuality in the red algae seems quite possible; at least, the sexuality of the red algae and of other algae may have had independent origins in the parasexuality of the bacteria. In having nuclei and plastids the red algae resemble the other groups of algae instead of the blue-greens, but these characters represent such obvious steps in an evolutionary ascent that they do not carry much

weight as indicators of relationship. Even if plastids and proper nuclei were considered to have originated only once, the divergence of the red algae from the remainder of the group must have occurred barely above the level of the Cyanophyceae.

The Florideophyceae are the more advanced of the two classes of red algae; and if this were the only class known, the relationships of the group might be questionable. The Bangiophyceae, however, are less highly modified, and some of the genera, which have blue-green chloroplasts and lack sexual processes and central vacuoles, are very suggestive of the Cyanophyceae. Some of these genera which recall the blue-green algae occur in fresh water. The evidence indicates that the blue-green algae are ancestral to the Bangiophyceae, and that the Florideophyceae are derived from the Bangiophyceae.

It has been customary to treat the Bangiophyceae and Florideophyceae as sub-classes of a single class, Rhodophyceae, but the differences between them are of the same order of magnitude as between other related classes of algae. Now that the red algae are generally regarded as constituting a distinct division, there is no reason why the two major groups should not be treated as classes instead of sub-classes. In this regard I follow Melchior (1954) and Copeland (1956).

FLAGELLATES AND THEIR ALGAL DESCENDANTS

Most algologists now accept the concept of Pascher that among the algae, other than Cyanophyceae and Rhodophyta, the unicellular flagellates represent a primitive type from which the other body forms are derived. A summary of this view is given by Smith (1950). In general, the idea is very probably correct, but Copeland's observations (1955) on the cytology of *Prasiola* raise a question as to its universal applicability. *Prasiola* is a thallose, non-flagellated genus which has the pigments of the Chlorophyceae and has usually been referred to that group. Cytologically, however, it is very suggestive of the Cyanophyceae, with a structure apparently more primitive than any of the known flagellated forms. Even if it turns out that *Prasiola* does have a vesicular nucleus, as Friedmann's studies (1960) imply, the cells appear to be cytologically less complex than those of more advanced groups of algae.

Another alga which indicates a connection between the Cyanophyceae and the Chlorophyceae is the thermal species treated by Geitler (1933) as *Cyanidium caldarium* (Tilden) Geitler, by J. J. Copeland (1936)

as *Pluto caldarius* (Tilden) J. J. Copeland, and by Allen (1954) as *Chlorella caldaria* (Tilden) Allen. According to Drouet and Daily (1956), these names have been misapplied to the species in question, which differs from Tilden's original *Protococcus botryoides* f. *caldarius* and is still nameless. The species in question occurs in hot springs at temperatures of 70 to 80 degrees C., within the temperature range of other thermal Cyanophyceae but far beyond the known tolerance of other Chlorophyceae. Miss Allen reports that "At times the pigments appear to be diffusely distributed throughout the cell, but in growing cultures most of the cells have the pigments contained in a single large plastid. An orange-red spot, suggestive of the eye spot of the Volvocales, has been observed in the cells of the Sonoma strain." Miss Allen does not definitely describe the nucleus, but she states that "On the basis of cell structure and mode of reproduction, the algae would be placed in the genus *Chlorella* of the Chlorophyceae." She also finds, however, that "an aqueous extract obtained by grinding cells with alumina and extraction of the ground mass with water contains a blue pigment which has an absorption spectrum identical with that of the phycocyanin of blue-green algae." After some further discussion, she concludes that "The weight of the evidence thus favors placing these algae in the genus *Chlorella*, leaving their pigmentation as an anomaly." She further notes that "*Chlorella caldaria* is the most thermophilic member of the Chlorophyceae on record."

It thus appears that there are at least two genera which combine in different ways some of the characters of the Cyanophyceae with some of the characters of the Chlorophyceae, and that these classes should, if possible, be placed somewhere near each other in the scheme of classification. It is here suggested that the first evolutionary dichotomy of the primitive plant stock with chlorophyll-a and β-carotene led on the one fork to the Cyanophyceae, and on the other to the Chlorophyceae. The characteristic 11-strand flagellum of the Chlorophyceae and their descendants may have been evolved from the separate unistrand flagella of the bacterial ancestors either before or after the divergence of the chlorophycean and cyanophycean lines. In either case, the Cyanophyceae must soon have lost whatever flagella their ancestors possessed, inasmuch as flagella of any type are wholly unknown among the Cyanophyceae and their descendants.

It has already been noted that all flagellates have flagella of the same basic structure. There are, however, several minor variations on

the general plan. The simplest type, usually called the whiplash type, lacks appendages of any sort, although the two central strands usually extend out beyond the nine peripheral ones. A second type, here called the pectinate type, has a single row of slender spreading appendages (mastigonemes); sometimes the flagellum is spirally twisted so that the mastigonemes do not all appear to be on the same side. A third type, here called the pinnate type, has two rows of mastigonemes, one on each side, like the barbs of a feather. The term "tinsel flagellum" is commonly applied to both the pectinate and pinnate types. The tinsel flagellum is a more effective locomotor organ than the whiplash flagellum and is presumably an evolutionary modification of it. Flagella of some protozoa appear to have mastigonemes all around, suggesting a bottle-brush, but this type has not yet been clearly demonstrated among the distinctly algal flagellates.

Excluding the Cyanophyceae and Rhodophyta, which, as we have seen, constitute another line of development, the Chlorophyceae are the most primitive class of algae, from which the other classes are presumably derived. The flagella of the Chlorophyceae, whether of motile gametes or motile spores or motile vegetative cells, are characteristically equal and of the whiplash type. Flagellated cells of other groups of algae, except the Charophyceae, generally have some or all of the flagella of the tinsel type; very often a single cell has two dissimilar flagella, one whiplash, the other tinsel. The familiar chlorophycean genus *Chlamydomonas,* with its large, solitary choroplast and two equal whiplash flagella, may well be the most primitive existing flagellate, scarcely if at all different from the hypothetical common ancestor of all existing flagellates.

If the relationships and origin of the green algae as here postulated are correct, the possession of a cell wall is a primitive character among the flagellates, and its absence is secondary. The Schizophyta, from which the Chlorophyceae are considered to be derived, characteristically have a cell wall, except for some special groups of bacteria such as the spirochaetes and the slime bacteria; all of the photosynthetic bacteria have cell walls. Although the bacterial cell wall is usually nitrogenous, the chemical composition varies a great deal in different kinds of bacteria and frequently includes some polysaccharides (Salton, 1956). A few bacteria definitely produce cellulose (Khouvine, 1933; Thimann, 1955), which is also a regular constituent of the walls of the Cyanophyceae.

The Charophyceae are universally regarded as derived from the Chlorophyceae. The only difference of opinion is the taxonomic rank at which the derived group should be received. Some consider it to form an order (Charales) within the Chlorophyceae; others regard it as forming a class (Charophyceae) coordinate with the Chlorophyceae, as is done here; still others maintain that it constitutes a distinct division (Charophyta). Most algologists are now agreed that ordinal status within the Chlorophyceae does not sufficiently emphasize the distinctness of the group in question. On the other hand, elevation of the group to divisional status does not reflect its undoubted relationship with the Chlorophyceae, and I therefore follow Smith (1938) in recognizing the Chlorophyceae, and Charophyceae as two classes constituting the division Chlorophyta.

The euglenoids are a well defined group of flagellates which appear to be derived directly from the chlorophycean flagellates. Their inclusion within the Chlorophyta, however, would effectively obliterate the distinctions among the Chlorophyta, Chrysophyta and Pyrrophyta, and if these several groups were put together the Phaeophyta could hardly be excluded. Such a drastic condensation would be wholly unacceptable to algologists, and it therefore becomes necessary to recognize the euglenoids as a distinct division (Euglenophyta) with a single class (Euglenophyceae).

The euglenoids, cryptomonads and chloromonads are alike in several respects, but it does not seem possible to group these into a descriptively definable division without bringing in also the Pyrrophyta, Chrysophyta and Phaeophyta. The only other obvious relatives of the cryptomonads are the Dinophyceae and Desmophyceae. I therefore follow Pascher (1914) and a number of later authors in referring the cryptomonads to the division Pyrrophyta as a class Cryptophyceae, coordinate with the classes Dinophyceae and Desmophyceae. The latter two classes are closely related to each other, and algologists are generally agreed that they must be held in the same division. Their relationship with the Cryptophyceae is admittedly more distant, but the latter class is hardly distinctive enough to warrant divisional status, and is better included in the Pyrrophyta than in any other division.

The recent discovery of phycobilin pigments in some of the cryptomonads (Allen, Dougherty and McLaughlin, 1959; Oheocha and Raftery, 1959; Haxo and Fork, 1959) is very interesting, but its phyletic import remains to be clarified. The only other organisms

known to have phycobilins are the red algae and blue-green algae, but these are otherwise so different from the cryptomonads that a close relationship is difficult to visualize.

Unpublished observations by J. J. A. McLaughlin disclose considerable variation in the distribution of mastigonemes on the flagella of dinoflagellates. This character, while apparently very useful in other groups, is evidently less stable in the dinoflagellates. Here, as elsewhere, taxonomic characters do not have established, inherent importance; they are only as useful as they prove to be in each individual instance in defining groups which have been perceived on the basis of all the available evidence.

The proper position of the Chloromonadophyceae will probably remain doubtful at least until their pigments are analyzed and their flagella carefully studied. Because they have neither starch nor cellulose and have not been demonstrated to possess the characteristic dinophycean xanthophylls, it seems unwise to refer the chloromonads to the Pyrrophyta at this time, although this disposition of the group has been suggested by Skuja (1948). On the other hand, there is nothing in the available evidence to controvert their being considered a near-basal group in the Chrysophyta, allied to the Xanthophyceae. The original definition of the class Xanthophyceae (under another name) by Luther (1899) included the chloromonads as an order. The characteristic statospores which are found in all the other classes of the Chrysophyta are unknown in the chloromonads, but this may be of no great significance, since many of the Xanthophyceae also lack statospores.

The position of the Xanthophyceae, Chrysophyceae and Bacillariophyceae as classes of a division Chrysophyta is widely accepted by algologists. The similarities, in pigmentation, food reserves, flagellar structure, wall structure and type of spore combine to make this a well marked group, as noted by Pascher (1914) and many later workers. The Xanthophyceae are the least modified of these three classes, and the most like the Chlorophyceae. Genera such as *Vaucheria* (Xanthophyceae) and *Botryococcus* (Chlorophyceae; see Belcher and Fogg, 1955) have had to be studied in considerable detail before their position as members of the Xanthophyceae or Chlorophyceae could be clearly ascertained.

Some algologists treat the Bacillariophyceae as a separate division, but I see no need for this. The characteristic structure and chemistry

of the cell wall, which make the diatoms so distinctive, are clearly foreshadowed in the Xanthophyceae, and the other special features of the diatoms scarcely require their segregation as a separate division. The relationship of the Bacillariophyceae to the Xanthophyceae and Chrysophyceae is so plain that it ought to be reflected in the taxonomic scheme, and the inclusion of the Bacillariophyceae in the division Chrysophyta poses no other problems to the general system.

The Phaeophyta (brown algae) are a well defined group which nearly all algologists now treat as a division. A common ancestry with the Chrysophyta is suggested by the flagella, as noted by Manton (1954); flagellated cells in both divisions characteristically have two flagella, one whiplash, one pinnate. Among the algae the pinnate flagellum is largely or wholly restricted to these two divisions.

The pigmentation of the brown algae suggests a relationship to both the Chrysophyta and the Pyrrophyta. All these groups have an excess of carotenoid pigments over chlorophylls, as compared to the Chlorophyta. Chlorophyll-c is known only in the Phaeophyta, Chrysophyta and Pyrrophyta. Fucoxanthin, the principal xanthophyll of the brown algae, occurs also in the Chrysophyceae and Bacillariophyceae, but is unknown among the Pyrrophyta.

Algologists are not agreed as to the number of classes of Phaeophyta which should be recognized. Kylin (1933) recognized three classes on the basis of life cycles. The Isogeneratae have similar sporophyte and gametophyte generations; the Heterogeneratae have dissimilar sporophytes and gametophytes, with the sporophyte always the larger; and in the Cyclosporae the gametophyte generation has been practically eliminated. Kylin's treatment has been widely adopted but has recently been challenged by Papenfuss. After initially accepting the three classes (1951a), he has concluded (1951b, 1955) that the Heterogeneratae represent at least two groups independently derived from the Isogeneratae and that the distinction between the Isogeneratae and Heterogeneratae is, therefore, un-natural. While continuing to admit the isolation of the Cyclosporae, he now prefers to recognize only a single class for the whole division, and he vigorously defends this point of view in personal conversation and correspondence.

The differences within the Phaeophyta are certainly as great as the differences between classes in other divisions, and some sort of analysis of this division into classes would seem to be desirable. In view of the generally admitted isolation of the Cyclosporae, this group may well

stand as a distinct class. The proper assortment of the remaining members of the division into one or more classes remains to be clarified; perhaps the Heterogeneratae should be broken up into two classes. For the present it will perhaps do no harm to continue to recognize the Isogeneratae and Heterogeneratae as classes, following Kylin.

An evolutionary pattern for the algal flagellates which fits the available evidence is as follows: Chlorophycean flagellates such as *Chlamydomonas,* with all flagella of the whiplash type, represent the most primitive group. The development of a row of mastigonemes on the flagellum, converting it into a more effective swimming organ, may have occurred only once. The euglenoids diverged from this line while the mastigonemes were restricted to a single row, and before any significant change in pigmentation had occurred. The gullet of the euglenoids is foreshadowed by the apical indentation around the flagella of a few green algae, for example, *Platymonas* and *Prasinocladus.*

The next significant step in the evolution of the remaining group was a shift in the proportions of the photosynthetic pigments, to more carotenoids and less chlorophyll, along with the development of some new kinds of carotenoids and chlorophylls. The number of flagella became stabilized at two, usually one whiplash and one tinsel, and the apical indentation was modified into a longitudinal ventral groove. The Pyrrophytan line diverged just after these steps, tending to retain the cellulose wall and starch food reserves of their chlorophycean ancestors. In the Cryptophyceae, one end of the ventral groove is often modified into a gullet; the Desmophyceae tend to lose the groove altogether; and in the Dinophyceae the groove takes on a spiral and eventually a transverse orientation.

The next step in the evolution of the remaining group (after the divergence of the Pyrrophytan line) was the development of a second row of mastigonemes on the tinsel flagellum, converting it to the pinnate type. Soon after this step, other products were substituted for starch as food reserves. The group then divided into two lines. One line retained cellulose as a principal cell wall constituent and went on to produce many multicellular plants; these are the brown algae. The other line dispensed with cellulose as a cell wall constituent, retaining the pectic compounds and eventually adding silica, and also dividing the cell wall into two overlapping halves. This line, which became the Chrysophyta, produced many unicellular algae but only a few small

multicellular ones. The longitudinal ventral furrow of the flagellated cells soon was eliminated in the main Chrysophytan line, although the chloromonads retained it. In the Phaeophytan line the furrow was modified into a broad shallow depression by reduction of one of the flanks, and this change was associated with the change in the position of the flagella from ventrally subterminal to lateral.

Part of the foregoing interpretation of algal evolution has been adapted from a paper by Chadefaud (1953).

FUNGI

The evolutionary origin and taxonomic status of the fungi have been debated among mycologists as long as the principle of organic evolution has been considered taxonomically significant, and opinion is still divided. A line of thought descending from Sachs (1874) holds that the Ascomycetes and Basidiomycetes are derived from the red algae, whereas the Phycomycetes are independently derived from other algae. An opposing line of thought, descending from DeBary (1884), holds that at least the Phycomycetes, Ascomycetes and Basidiomycetes collectively form a monophyletic group in which the Phycomycetes occupy a basal or near basal position.

The most significant new evidence on the relationships of the fungi lies in the structure of the flagella in those forms (Myxomycetes and Phycomycetes) which produce flagellated cells. Among the Phycomycetes there are three types of flagellated cells: *a*) biflagellate cells with one whiplash and one tinsel flagellum; *b*) uniflagellate cells with a tinsel flagellum; and *c*) uniflagellate cells with a whiplash flagellum (Couch, 1941). The tinsel flagellum is generally of the pinnate type, although Couch reports that in one species, *Olpidiopsis saprolegniae*, it is sometimes pinnate and sometimes pectinate. Among the Myxomycetes flagellated cells are apparently always biflagellate, the flagella being unequal and both of the whiplash type; the shorter flagellum is often so small as to be easily overlooked (Ellison, 1945; Elliott, 1949).

Making use of the information provided by Couch, Bessey (1942) has suggested that the Phycomycetes are derived from flagellates of the general Xanthophycean type. It will be recalled that the Chrysophyta, including the Xanthophyceae, characteristically have two dissimilar flagella, one whiplash, one tinsel (pinnate). Bessey's concept here appears to be essentially sound, although I would suggest that the divergence may have occurred a little earlier in the Chrysophytan line,

before the change of the tinsel flagellum from pectinate to pinnate had become fully stabilized. Under Bessey's concept, with or without the modification proposed here, the Phycomycetes with uniflagellate cells would be derived from biflagellate types, by loss of either the tinsel or the whiplash flagellum. The filamentous aquatic members of the Phycomycetes would, under this hypothesis, be a later modification from chytrid-like types with two flagella, and the Zygomycetes would be derived from filamentous Oomycetes.

The secondary zoospores of the Saprolegniales are described by Bessey (1950, p. 105) as "kidney-shaped or resembl[ing] a grape seed with the two flagella arising in the groove, usually nearer the more pointed end than the base. One flagellum, of the tinsel type, is directed forward while the whiplash type flagellum is directed posteriorly." As thus described, these secondary zoospores are in some respects suggestive of mature cells of some of the cryptomonads, especially as regards the groove and the insertion of the flagella. This situation would seem to strengthen the case for deriving the flagellated Phycomycetes from near the point at which the Pyrrophytan and Chrysophytan lines diverge, rather than well within the Chrysophytan line as suggested by Bessey.

The similarity between the alga *Vaucheria* and the phycomycetous genus *Saprolegnia* is well known. *Vaucheria* was, until recently, generally included with the Chlorophyceae, and this class was often regarded as ancestral to the Phycomycetes. The flagella of *Saprolegnia* are, however, much more like those of the Chrysophyta than those of the Chlorophyceae, so that a direct derivation of *Saprolegnia* or any other Phycomycete from the Chlorophyceae now seems unlikely. The recent demonstration that *Vaucheria* has typical Chrysophytan flagella (Koch, 1951) and properly belongs in the Xanthophyceae instead of the Chlorophyceae (Smith, 1955) tends to restore cogency to the suggestion that *Saprolegnia* may be derived more or less directly from it. This idea is not so very different from Bessey's idea of a derivation of the Phycomycetes from flagellates, since in both cases the emphasis is on the Xanthophyceae as the ancestral or near-ancestral group.

It may be noted in passing that both the Saprolegniales, which are biflagellated, and the biflagellated chytrid-like types have considerable cellulose in the cell wall, and that in both the filamentous and the chytrid-like Oomycetes the cellulose tends to give way to fungus chitin in the uniflagellate derivative forms. The Zygomycetes, the Ascomycetes

and the Basidiomycetes have chitinous walls ordinarily without significant quantities of cellulose.

The relationship of the Basidiomycetes to the Ascomycetes, and the ultimate derivation of the Phycomycetes from flagellates of more or less chrysophytan or pre-chrysophytan type (either directly or through filamentous algal intermediates) may be considered to be fairly well established. Competent opinion remains divided as to whether the Ascomycetes are derived from the Phycomycetes or from the Rhodophyta. My own belief is that those who see a relationship between the Phycomycetes and the Ascomycetes have the better of the argument. The widespread occurrence of glycogen as the carbohydrate food reserve, and of chitin as the wall material, in the Phycomycetes, Ascomycetes and Basidiomycetes tends to unite these classes and to separate them from all of the suggested algal ancestors, as does also the general tendency for karyogamy to be delayed until long after plasmogamy. The change from cellulose to chitin occurs within the Phycomycetes, as does the beginning of the tendency for delay of karyogamy. In many of the filamentous Phycomycetes there is a considerable time-lag between plasmogamy and karyogamy, but there are no intervening nuclear divisions. In the Basidiomycetes and the vast majority of the Ascomycetes the delay has been expanded, allowing a series of mitoses between plasmogamy and karyogamy, so that there is a dicaryotic stage of greater or lesser length.

Perhaps the best bridge between the Phycomycetes and the Ascomycetes is provided by the genus *Dipodascus,* as pointed out by Atkinson (1915). *Dipodascus* lacks a definite fruiting body, and it produces numerous ascospores in an ascus. The ontogeny of the ascospores is typical of the Ascomycetes, and mycologists are generally agreed that the genus is properly referred to this class. *Dipodascus* also differs from most other Ascomycetes in lacking the characteristic croziers by which the developing asci proliferate, and it further resembles the Phycomycetes in that no mitotic divisions intervene between plasmogamy and karyogamy. It is thus clear that *Dipodascus* tends to bridge the gap between the Phycomycetes and the Ascomycetes. The difference between the coenocytic hyphae of the Phycomycetes and the septate hyphae of the Ascomycetes is of little significance as a barrier to relationship. Many of the Phycomycetes tend to develop septa in age, and in many of the Ascomycetes, including *Dipodascus,* the hyphal segments delimited by the septa are multinucleate.

The most characteristic single feature of the Ascomycetes, and the only one which separates them absolutely from the Phycomycetes, is the ontogeny of the ascospores, which develop in such a way that some of the original cytoplasm of the ascus is not included in any of the spores, remaining instead as epiplasm. This is clearly a specialized feature, and it sets the Ascomycetes off from the red algae just as sharply as from the Phycomycetes.

In summary, there is no good reason why the Ascomycetes could not have been derived from the Phycomycetes, and there are cogent reasons for retaining the Phycomycetes, Ascomycetes and Basidiomycetes as a natural group. The characters which tend to hold these three classes together as a natural phylad are least developed or most subject to exception among the Phycomycetes, which must be considered the basal group.

Among the classes of fungi here accepted, only the position of the Myxomycetes remains to be discussed. The only obvious near relatives of the Myxomycetes are the Phycomycetes, especially the chytrids and their immediate allies. The order Plasmodiophorales appears to form a connecting link between the two classes. The long-standing difference of opinion on the position of the Plasmodiophorales continues even up to the present time, with some authors, such as Bessey (1950) and Alexopoulos (1952), preferring to associate them with the Myxomycetes, whereas others, such as Sparrow (1943, 1960), refer them to the Phycomycetes. This continuing difference of competent opinion is eloquent testimony as to the transitional position of the Plasmodiophorales.

The structure of the flagella furnishes perhaps the most important new evidence on the relationships of the Plasmodiophorales. Sparrow (1960) reviews the studies of Ellison (1945) and later authors which have shown that the Plasmodiophorales characteristically have two unequal whiplash flagella, like the Myxomycetes, and unlike all other flagellated organisms. Sparrow concludes (p. 770) that the flagellar structure "gives weight to the theory that this group [the Myxomycetes] has affinities with the Plasmodiophorales." He continues to retain the Plasmodiophorales in the Phycomycetes, however, following his own earlier (1943) treatment.

I do not delude myself that the position of the Plasmodiophorales can be conclusively established in a paper such as this. In my opinion, however, the weight of the evidence is that they should be associated

with the Myxomycetes, as a group morphologically and phyletically transitional toward the Phycomycetes. Some authors who consider the Myxomycetes to belong to a division or subdivision apart from the true fungi (e.g. Smith, 1955) prefer to elevate the Plasmodiophorales to the status of a class coordinate with the Myxomycetes proper. I have no great objection to such a disposition of the Plasmodiophorales, but I doubt that it is necessary. For the present, at least, I am content to allow the Plasmodiophorales to remain as a well marked order of the Myxomycetes.

The status of the small orders Acrasiales and Labyrinthulales is more doubtful. The Labyrinthulales could probably be accommodated among the Protozoa without great difficulty. If they were retained within the Myxomycetes they would have to lie near the Plasmodiophorales. The swarm cells, however, are uniflagellate or without flagella, and the definition of the Myxomycetes would be facilitated if this group could be excluded. In any case, there seems to be no present need to set up a separate class for them, and therefore they need not be further considered in this paper. The Acrasiales have been considered by Smith (1955) and others to constitute a distinct class coordinate with the Myxomycetes. This may ultimately prove to be the best treatment, but in the present state of uncertainty as to their relationships I prefer to append them to the Myxomycetes, without altering the formal definition of the latter group.

The presence of two distinctly unequal flagella, both of the whiplash type, appears to be the only distinctive feature of the Myxomycetes which permits them to be sharply separated from the Phycomycetes, among those genera which are otherwise doubtful or transitional between the two classes. This flagellar constitution is in fact apparently unique. To the best of my knowledge, all groups of flagellates so far studied which have two unequal flagella have at least one of the flagella of the tinsel type. There is, therefore, no advantage in seeking a derivation of the Myxomycetes from flagellated ancestors independently of the derivation of the Phycomycetes. The most likely hypothesis seems to be that the Myxomycetes and Phycomycetes have a common ancestry among the flagellates, but that the Myxomycetes have lost the mastigonemes from the tinsel flagellum. If the chytrid-like Phycomycetes with two dissimilar flagella and with cellulose walls (i.e. the order Lagenidiales) are considered to be the most primitive existing Phycomycetes, then the Myxomycetes might well be considered to be de-

rived from the very base of the Phycomycete line, or from pre-Phycomycete ancestors.

Although their relationship to the Phycomycetes is now fairly clear, the Myxomycetes do stand out as a separate group in contrast to the group consisting of the Phycomycetes, Ascomycetes and Basidiomycetes. There is, therefore, some value and no harm in recognizing two subdivisions of fungi, one for the Myxomycetes and one for the three remaining classes. Such treatment also permits elevation of the Plasmodiophorales to the status of a class, by those who wish to do so, without obscuring their relationship to the Myxomycetes.

The class Archimycetes, as defined by Gäumann (1926; Gäumann and Dodge, 1928), has no raison d'être. The group is considered to consist of "naked, often amoeboid forms which develop holocarpic reproductive organs by division of the whole thallus", and the statement is made that in the Phycomycetes "The thallus, in contrast to that of the Archimycetes, is surrounded by a membrane". In discussing the Chytridales, which are allowed to remain in the Phycomycetes, Gäumann notes that "the lowest forms are holocarpic; i.e. the whole thallus forms a fructification." The critical character for the Archimycetes, therefore, resolves itself to the presence or absence of a wall.

Gäumann considers the Archimycetes to consist of four families, the Olpidiaceae, Synchytriaceae, Plasmodiophoraceae and Woroninaceae. The Olpidiaceae and Synchytriaceae do develop definite walls (Bessey, 1950) after the naked zoospore or zygote has penetrated the host cell. Inasmuch as the zoospores of the chytrids are also naked, developing a wall only after settling down onto the host, the difference between the chytrids (Phycomycetes), on the one hand, and the Olpidiaceae and Synchytriaceae (Archimycetes), on the other, thins down to a slight postponement of wall formation in the latter groups. Some of the chytrids, such as *Diplophlyctis*, become wholly intracellular, and indeed Gäumann's description of the process by which *Diplophlyctis* becomes intracellular is essentially similar to his description of the same process in *Olpidiopsis saprolegniaceae* (Olpidiaceae). It is thus clear that the Olpidiaceae and Synchytriaceae do not differ fundamentally from forms which Gäumann retains in the Phycomycetes, and these two families could easily be accommodated in the Phycomycetes.

The Plasmodiophoraceae and Woroninaceae are more or less distinctly plasmodial, as called for in Gäumann's preliminary characterization of the Archimycetes. The Plasmodiophoraceae, as we have noted,

resemble the Myxomycetes in flagellar structure. There has been some confusion regarding the actual identity of the organisms referred to the Woroninaceae, with consequently conflicting reports as to their structure. A detailed study of an organism identified as *Woronina polycystis* (the type species of *Woronina*) by Goldie-Smith (1954) shows it to be essentially similar to the Plasmodiophoraceae in flagella as well as other features, and Sparrow (1960) has followed Goldie-Smith in referring *Woronina* to the Plasmodiophoraceae.

Thus, of the four families referred to the Archimycetes by Gäumann, two would be at least as well placed in the Phycomycetes as in the Archimycetes, even if the Archimycetes were retained as a group; a third (the Plasmodiophoraceae) is more or less transitional between the Phycomycetes and Myxomycetes but perhaps most closely related to the latter; and the fourth is not clearly distinguished from the third. The position of the Archimycetes as a separate class has been rejected by Fitzpatrick (1930) and Martin (1932) among others, and even Gäumann now admits its artificiality. The most recent (1952) edition of his text contains the statement, "Certainly the Archimycetes, as the various types of flagella suggest, represent a phylogenetically heterogeneous group." The class Archimycetes should, therefore, be abandoned.

The Actinomycetes have sometimes been considered to be fungi, or to be a transitional between the fungi and the bacteria. They have no obvious relatives among the fungi, however, while they are connected to undoubted bacteria by the Mycobacteriaceae, which have been included in the Actinomycetes by some authors and in the Eubacteriales by others. The complex type of nucleus which characterizes all major groups of organisms except the schizophytes has not been demonstrated to occur in the Actinomycetes, and the flagellar structure of the gonidia, as reported by Couch (1949), is apparently that of bacteria, not of other flagellated organisms. In my opinion, the Actinomycetes bear no close relationship to the fungi and should be included instead among the bacteria.

GENERAL FEATURES OF EMBRYOPHYTES

Having concluded the Thallophyta, we turn now to the Embryophyta. The Embryophyta form a well-marked group with many morphological, anatomical and physiological features in common, and it is clear that the Embryophyta are ultimately derived from the Thallophyta.

The pigments of the chloroplasts of the Embryophyta are chloro-

phylls-a and -b, β- and usually α-carotene, and several xanthophylls, generally including lutein, cryptoxanthin, neoxanthin and zeaxanthin (Strain, 1944). Chlorophyll-a is the principal chlorophyll, β-carotene is the principal carotene, and lutein is usually the principal xanthophyll. The carotenoid pigments are masked by the more abundant chlorophylls. The most common carbohydrate reserve is starch. The primary cell wall is composed largely of cellulose. Flagellated cells bear only the whiplash type of flagellum. In all these respects the Embryophyta resemble the green algae (Chlorophyceae) (Strain, 1944, 1951; Smith, 1955; Manton, 1952), and the green algae are widely believed to be ancestral to the Embryophyta.

The Embryophyta differ from the green algae and from most Thallophyta in that the normal life cycle of the Embryophyta shows a well developed alternation of generations in which the sporophyte begins its development as a parasite on the gametophyte. Sometimes the gametophyte is retained on the old sporophyte, and is so much reduced that it serves only briefly as a means of transferring food from the old sporophyte to the new one. The only chlorophyllous thallophytes with a definite sporophyte attached to the gametophyte are some of the red algae, and these are so different from the Embryophyta in other respects that no close relationship seems possible.

Many of the thallophytes produce one or more kinds of asexual spores (i.e., mitospores) in addition to, or instead of, the sexual spores (i.e., meiospores) which are formed as a result of reduction division and are part of the normal sexual life cycle. The embryophytes regularly produce sexual spores, and they never produce any other sort of spore. Asexual reproduction, when it occurs among the Embryophyta, does not involve formation of spores. The term "sexual" is here used in the broad sense to apply to phenomena related to nuclear fusion and reduction division, regardless of whether or not the gametes are distinctly male and female.

All of the less highly modified divisions of the Embryophyta have multicellular antheridia and archegonia in which the gametes are borne. Except as noted in the Charophyceae, the gametes of the Thallophyta are borne in unicellular gametangia which may or may not be differentiated as antheridia and oogonia. The multicellular sexual structures of the Charophyceae do not closely resemble those of the Embryphyta, being merely analogous to instead of homologous with them. The so-called multicellular or plurilocular gametangia of the brown

algae are mere aggregations of unicellular gametangia, without the sterile jacket that characterizes the multicellular gametangia of the embryophytes.

BRYOPHYTES

There are two principal opposing theories as to the nature of the green algal ancestors of the embryophytes and the general course of evolution of the embryophyte subkingdom. According to the homologous theory, the ancestor of the embryophytes was a green alga with isomorphic alternation of generations. *Fritschiella* has been suggested (Singh, 1954) as a terrestrial chlorophycean genus with isomorphic alternation of generations which shows the potentialities necessary for evolutionary development along the lines of the embryophytes; this suggestion has received favorable attention from a number of students of plant evolution. The primitive embryophyte is believed to have had similar gametophyte and sporophyte generations, and from this type evolution has proceeded in two directions. In one line the sporophyte became essentially parasitic on the gametophyte, losing much or all of its photosynthetic capacity and coming to be scarcely more than a stage in the reproduction of the gametophyte. The bryophytes represent this line of development. In the other line the sporophyte became the dominant generation, and the gametophyte was reduced, eventually becoming merely a step in the reproduction of the sporophyte. The vascular plants represent this line of development.

According to the antithetic theory of land plant evolution, the ancestor of the embryophytes was a green alga in which the zygote was the only diploid cell. The sporophyte is regarded as an entirely new structure interposed between two successive gametophyte generations, and evolutionary advance consisted of progressive elaboration of the sporophyte and eventual reduction of the gametophyte. Under the antithetic theory the bryophytes are regarded as an intermediate step from the green algae toward the vascular plants.

The accumulation of evidence during the past several decades has favored the homologous theory. At the time that Bower (1890, 1908) was developing and expounding the antithetic theory, all or nearly all of the green algae in which sexual reproduction was known had only a single diploid cell in the life cycle; many genera with isomorphic alternation of generations are now known. Evidence from comparative morphology of the bryophytes themselves suggests that forms with very small sporophytes have been derived from ancestors with larger

sporophytes, and more and more bryologists have been interpreting the bryophytes in terms of reduction series. By 1935 Bower himself felt it necessary to modify the antithetic theory substantially in the direction of the homologous theory, and the familiar classical antithetic theory is now of little more than historical interest.

One of the most convincing bits of evidence pointing to the derivation of the bryophytes from ancestors with more complex sporophytes is the presence of stomates on many bryophytic sporophytes in which they have little or no functional importance. The stomate—guard-cell apparatus is a complex evolutionary adaptation to the need of a land plant for access of air to internal photosynthetic tissues, without excessive transpiration during periods of water deficiency. It is not likely that such a mechanism would arise in advance of the need.

None of the three classes of bryophytes can be considered directly ancestral to any of the others. Regardless of what view is taken as to the evolutionary history of the group, each class is advanced in some features and more primitive in others. There has probably been an evolutionary progression from erect gametophytes bearing three rows of equal phyllidia ("leaves"), to dorsiventral gametophytes with the ventral row of phyllidia reduced or wanting, to strictly thallose gametophytes without phyllidia. The thallose gametophyte of the Anthocerotae is thus interpreted as among the most "advanced" of the division, while the sporophyte is the least reduced and most primitive in the division. Even if the older viewpoint is retained and the sporophyte of the Anthocerotae is considered to be an advance toward the condition of the vascular plants, the presence of pyrenoids in the chloroplasts of the Anthocerotae is still a primitive character not shared by other members of the division.

An interesting feature which links the Anthocerotae to the vascular cryptogams, and separates all of these groups from the Musci and Hepaticae, is the ontogeny of the archegonium. In the Musci and Hepaticae the whole archegonium is derived by a series of divisions from a primary archegonial cell. In the Anthocerotae and all other archegoniates, the cells lining at least the lower part of the venter of the archegonium are ordinary or more or less modified vegetative cells of the gametophyte, not derived from the archegonial initial.

The status of the Anthocerotae as a distinct class coordinate with the Hepaticae and Musci is now so widely accepted by bryologists, as well as being so fully in accord with the evidence, that it seems un-

necessary to defend it in detail here. The view here presented of the position of several groups of bryophytes with regard to the psilophytes and green algae is in accord with that of Mehra and Handoo (1953).

VASCULAR PLANTS

Botanists are now generally agreed that the psilophytes are ancestral or near-ancestral to all of the other vascular plants. Some, such as Tippo (1942), go so far as to recognize only a single division (or phylum) of vascular plants, the Tracheophyta, and this view is becoming popular in American textbooks. In my opinion, however, such a treatment minimizes the differences within the group; so large and varied a division is scarcely comparable to the other recognized divisions of plants. This is admittedly a matter of taste, though perhaps no more so than the insistance of algologists that the Euglenophyta, Chlorophyta, Phaeophyta, Pyrrophyta and Chrysophyta should not be included in a single division.

One of the currently most popular treatments of the vascular plants is to recognize four major groups—the Psilopsida, Lycopsida, Sphenopsida and Pteropsida. Among those who use this scheme are Eames (1936) and his followers. There seems to be no doubt that the Lycopsida and Sphenopsida represent natural groups. I propose to treat these as divisions, under the names Lepidophyta and Calamophyta, respectively, as originally suggested by Bessey (1907). In recent years this treatment has been adopted by Smith (1955) among others.

The position of the modern Psilotales as more or less direct descendants of the Psilophytales, instead of as close allies of any of the other modern groups, seems to be well established. If the Calamophyta and Lepidophyta are to be treated as divisions, then the Psilophyta must also take divisional status. Whether the modern psilophytes should be placed in the same taxonomic class within this division as their Devonian and Silurian ancestors is perhaps a matter of taste. The case for distinguishing the modern Psilotales and some of their fossil relatives from the Psilophytales at a higher taxonomic level is well presented by Nemejc (1950), and such a distinction would do no harm, but I am not convinced of the need for it.

The Pteropsida have been contrasted to all the other vascular plants because of their mostly large leaves that are associated with leaf-gaps in the stele. This distinction seemed particularly significant at a time when it was thought to reflect a basic difference in the origin of mega-

phylls (Pteropsida) and microphylls (all other vascular plants). Megaphylls were supposed to represent modified branch stem systems, whereas microphylls were supposed to be mere enations arising de novo from the stem (Bower, 1908).

The origin of pteropsidan megaphylls as modified branch stem systems seems to be abundantly confirmed by the fossil evidence as well as by the comparative morphology of modern plants. In familiar American texts the evidence is presented by Arnold (1947) and Smith (1955). It is now almost equally plain, however, that the microphylls of the Calamophyta (Sphenopsida) likewise represent modified branch stem systems instead of mere enations. The leaves of many fossil calamophytes are dichotomously branched, like psilophyte stems, or have a dichotomously branched vein system, and the microphyllous structure of the modern genus *Equisetum* is clearly due to reduction. Some of the evidence supporting this conclusion is presented by Zimmerman (1930), Lam (1948a) and Nemejc (1950).

Although the Calamophyta do not have leaf-gaps in the pteropsidan sense, the stele is broken up into definite vascular bundles. In some of the fossil Calamitales the leaf-traces diverge directly from the vascular bundles without disturbing the continuity of the latter. In all of the modern forms the bundles are offset at each node, and it requires careful study to show that the gap in the central cylinder above each leaf-trace is not a proper "leaf-gap". If the leaf-trace were to become enlarged so as to be as thick as the nodal ring—surely no great evolutionary change—the interfascicular gaps would have all the anatomical features of leaf-gaps.

According to the controversial telome theory of Zimmerman (1930), which is gaining increasing acceptance, even the microphylls of the Lycopsida represent modified branch stems rather than enations. Although the Lycopsida do not have leaf-gaps, many of them do have dissected steles; the gaps are merely not associated with the leaves.

With the presumed evolutionary significance of the distinction between megaphylls and microphylls dissipated, the question properly arises as to whether the presence of leaf-gaps is a sufficiently important character to hold the Pteropsida together as a natural group. The answer is, *almost certainly not*. It is of course well known that the leaf-gaps are wanting from some of the more primitive, protostelic ferns; if there is no pith there can scarcely be a leaf-gap. What may not be so well known is that some of the Cordaitales, as well as some of the

pteridosperms (e.g. *Lyginopteris*), had dissected steles without leaf-gaps, the vascular bundle continuing upward beyond the leaf-trace without interruption (Arnold, 1947). In this respect these steles resemble those of some of the Calamitales as previously described. I do not suggest that there is any very close relationship between the Calamitales and the gymnosperms, but rather that the presence or absence of leaf-gaps cannot properly be used as the sole character to mark off a major taxon of vascular plants.

There is evidently a general evolutionary tendency for the primitive protostele to become dissected into a series of vascular bundles, with or without a direct relation between the leaf-traces and the gaps. Dissected steles are no novelty even among the Lycopsida, as anyone will soon discover if he looks at a standard commercial slide of a *Lycopodium* stem in the expectation of seeing a typical protostele. It thus appears that the evolutionary tendency toward dissection of the stele may or may not lead to the formation of leaf-gaps, and that leaf-gaps could well have been independently developed by the ferns, pteridosperms and Cordaitales. Therefore any assumption of a close relationship among these groups should be based on, or at least bolstered by, other evidence. The proper taxonomic rank at which the ferns should be received can best be understood after a consideration of the gymnosperms.

Most recent students of gymnosperms, including Chamberlain (1935), Buchholz (1946), Gaussen (1941-52), Arnold (1948) and Florin (1952), agree that the gymnosperms (with the exception, for some authors, of the Chlamydospermae) fall into two major groups, the cycadophytes and coniferophytes, that these two groups are distinct as far back as the fossil record provides any evidence, and that the cycadophyte line derives from near the base of the ferns, through the pteridosperms. In some respects the differences between the two lines become more obviously important among the fossils than among the living species. The female cones of cycads do not look so very different from the female cones of some conifers, but the cycad cone scale is modified from a leafy pteridospermous megaphyll with marginal ovules, whereas the conifer cone is now regularly interpreted as derived from the cone cluster of the Cordaitales, in which latter the ovules are terminal on telome-like appendages of the cone axis. Schoute (1925) is doubtless correct in pointing out that the ovules of the Cordaitales are borne on the primary appendages of the cone axis, in-

stead of on shoots axillary to those appendages as had previously been believed, but in any case the ovule-bearing structure of the Cordaitales is quite different from that of the pteridosperms. Sahni's suggestion (1920) that the cycadophytes are phyllosporous and the coniferophytes stachyosporous may be subject to philological quibbling, but in substance it is sound. The implication is that the coniferophytes and cycadophytes do not have a common ancestor short of the psilophytes.

On the basis of the fossil record, Nemejc (1950) argues that the conifer leaf represents a minor branch system, more nearly comparable in that regard to the sphenopsid leaf than to the pteropsid leaf, which is generally conceded to be derived from a major branch system. (Florin's (1951) illustrations of the bifid to dichotomously lobed leaves of such paleozoic conifers as *Lebachia, Buriadia* and *Carpentieria* are very instructive in this regard). Nemejc concludes that the derivation of the coniferophytes from the psilophytes represents "an utterly independent origin, an evolutionary line without any relations either to the paleozoic Pteridosperms or to any group of the ferns." Unfortunately his system as presented does not reflect this conclusion, inasmuch as he recognizes a group Gymnospermae (taxonomic status unspecified) composed of two lesser groups, the Cycadophyta and Coniferophyta. Florin (1952) also emphasizes the difference between the leaves of the cycadophytes and coniferophytes, and in 1955, speaking of the Cordaitales, he concluded that "It seems probable that they were derived, independently of the pteridosperms, from primitive vascular plants of the general psilophyte type."

It has already been noted that the existence of fossil pteridosperms and fossil Cordaitales without leaf-gaps pushes any possible common ancestry for these groups back into the pre-leaf-gap evolutionary stage and thus presumably not far, if at all, above the psilophyte level. Thus the positive evidence from the structure of stems, leaves and cones combines with the negative evidence of the absence of convergence among the fossils to show that the gymnosperms are not a natural group. Any taxon which includes both the coniferophytes and the cycadophytes must also include the psilophytes as well as the ferns, and any taxon which includes these four groups might better be expanded to include all of the vascular plants. Unless one wishes to include all vascular plants in a single division, the coniferophytes must take divisional status.

The relationship of the cycadophytes to the ferns is so generally

conceded that it requires no documentation here. Likewise the derivation of the ferns from the psilophytes, and the interpretation of the fern leaf as a modified major branch system. It should be emphasized, however, that the dichotomy between the ferns and the cycadophytes occurred very nearly at the evolutionary base of the ferns, as witnessed inter alia by some pteridosperm fossil without leaf-gaps. If the coniferophytes are treated as a division, then in the interests of a balanced treatment the cycadophytes should also be treated as a division, leaving the ferns perforce as another division.

The proper name to use for the ferns in divisional status is a matter of some difficulty. The most obvious possibility is Pteridophyta, but this name has been so widely used to cover all vascular cryptogams that an attempt to restrict it to non-strobiloid vascular cryptogams with megaphylls and usually with leaf-gaps is an invitation to confusion. Names above the rank of an order are excluded from the principle of priority under the rules of nomenclature, and there is, therefore, no legal barrier to the use of another name. G. M. Smith's (1955) substitution of the name Pterophyta for Pteridophyta sens. strict. merely introduces a grammatical error, properly subject to correction under rules. The correct combining form of *Pteris* is Pterid-, not Pter-. The only other familiar classical term for ferns in general is ***Filix,*** reflected in such botanical names as Filices and Filicinae. The name Filicophyta, here introduced as a divisional name for the ferns, is admittedly a linguistic hybrid with a Latin stem and a Greek suffix, but it is at least unequivocal and not subject to correction under the rules.

The number of classes of Filicophyta and Cycadophyta should cause no difficulty; most botanists are agreed that there is no more than one class in each group. The Coniferophyta are another matter. Florin (1948, 1955) evidently considers the Coniferales, Ginkgoales, Taxales and Cordaitales to constitute distinct classes, although he does not present a formal system. Some authors, Johansen (1951) for instance, have gone so far as to recognize a phylum Ginkgophyta, coordinate with the Coniferophyta. The phylum, of course, has no nomenclatural status under the rules of botanical nomenclature, the proper and equivalent category being the division. Although I agree with Florin that the Coniferales, Taxales, Ginkgoales and Cordaitales are coordinate groups that collectively constitute a larger group, I see no need to consider them as separate classes. A single class with four orders will adequately meet taxonomic needs.

A proper consideration of the status of the Chlamydospermae requires an evaluation of the taxonomic significance of differences in the stomatal apparatus. In recent years it has become customary to lay considerable stress on the difference between haplocheilic and syndetocheilic stomates in the gymnosperms, following Florin (1931). The difference boils down to whether the stomatal mother cell gives rise only to the guard cells (haplocheilic type) or to the guard cells plus the cells which flank them laterally (syndetocheilic type). Ordinarily the two types are different in appearance: In the syndetocheilic type the cell which flanks the guard cell is usually about the same length as the guard cell and is obviously different from the other epidermal cells; in the haplocheilic type the cell or cells which flank the guard cell are often indistinguishable from ordinary epidermal cells, or they may be different from other epidermal cells but still not isometric with the guard cell. Many haplocheilic stomates are clearly recognizable as such from the mature morphology, and Florin classifies fossils as well as living specimens into one or the other category. According to Florin, the pteridosperms, Cycadales, Cordaitales, Coniferales and *Ephedra* are characteristically haplocheilic, whereas the Bennettitales, *Welwitschia* and *Gnetum* are characteristically syndetocheilic.

I am not convinced that this difference has any *inherent* taxonomic value, nor that the two types can always be distinguished without direct observation of the ontogeny. Arnold (1953) has correctly noted that in the conifers stomates which are ontogentically haplocheilic sometimes resemble the syndetocheilic type at maturity. This is evident from Florin's own drawings. Both haplocheilic and syndetocheilic stomates occur in the angiosperms. The "ranunculaceous" stomatal type, as described by Solereder (1908), is haplocheilic, whereas the "rubiaceous" type is syndetocheilic. Both of these types, as well as some others, are widely distributed among angiosperms, both types often occurring in the same family or order. Solereder also describes a "false rubiaceous" type which resembles the rubiaceous type at maturity but is ontogentically haplocheilic (in Florin's terminology). Metcalfe and Chalk (1950) have emphasized that in the dicotyledons stomates of similar morphology may differ in their ontogeny, and as a practical matter they have based their descriptions on the mature morphology rather than the ontogeny.

Florin interprets the syndetocheilic stomatal type as being derived from the haplocheilic, and with this I concur. It seems to me, however,

that this is an evolutionary change which might be expected to occur repeatedly in different groups. Haplocheilic stomates which morphologically simulate syndetocheilic ones would seem to be poised on the brink of transformation to syndetocheily.

The ontogeny of the stomates is merely one more character to be considered in arriving at a taxonomic conclusion. As I have previously (1957) noted, no taxonomic character has an inherent, fixed importance. Each character is only as important as it proves to be in any particular instance in defining a group which has been perceived on the basis of all the available evidence.

The relationships and taxonomic status of the Chlamydospermae (*Ephedra, Gnetum, Welwitschia*) have excited a great deal of investigation and taxonomic controversy. Recent opinion tends to hold that each of these genera should be placed in a family and order of its own, and with this I am inclined to agree. The differences among these three types have led many botanists to question their relationship to each other, but I agree with those students, such as Chamberlain (1935), who hold that they have too many features in common to permit their ultimate disassociation. They have vessels in the secondary wood; cones of both sexes are compound; the ovules have two integuments with at least the inner integument forming a very long micropylar tube; the leaves are opposite; the embryo has two cotyledons; and there are no resin canals. The xylem vessels and compound male cones are not found in any other gymnosperms, nor are bitegminous ovules, unless the epimatium of the Podocarpaceae is interpreted as an integument. (The evolutionary origin of the outer integument from strobilar bracts, as explained by Eames (1952), does not negate its tegumental nature, especially inasmuch as the inner or solitary integument of the whole division may well have arisen in much the same way (Florin, 1952)). The opposite leaves, dicotyledonous embryos and lack of resin canals are also more or less uncommon among other gymnosperms, but not unique.

Gnetum and *Welwitschia* further differ from all other gymnosperms in the absence of an archeogonium. In *Welwitschia* a specialized cell which is probably homologous with the archegonial initial functions directly as an egg. In *Gnetum* fertilization takes place while the female gametophyte is still in the free nuclear condition, with one or more of the nuclei becoming associated with some differentiated cytoplasm and functioning as eggs.

In their simple leaves, well developed secondary growth and compound female cones the Chlamydospermae are suggestive of the Coniferae, and these characters tend to separate them from the cycadophytes. Eames (1952) has interpreted the male and female cones of *Ephedra* as homologous with the cone-clusters of the Cordaitales, and I believe this interpretation is essentially correct. It has already been noted that the female cones of the Coniferales are also now generally interpreted as homologous with female cone-clusters of the Cordaitales, but the condensation evidently occurred independently in the two groups. Although Eames pointedly refuses to do so, I see no reason why his interpretation of the cones of *Ephedra* should not be extended to the basically similar cones of *Gnetum* and *Welwitschia*. The hermaphrodite "flowers" observed by Mehra (1950) in some individuals of *Ephedra intermedia* furnish a further link between *Ephedra* and *Welwitschia*. In *Welwitschia* the male "flowers" have a sterile terminal ovule. This feature seems to suggest that the ancestors of the Chlamydospermae had a bisporangiate strobilus. In personal conversation Mehra expresses the opinion that the Chlamydospermae have been derived from pre-cordaitalean coniferophyte ancestors.

I believe the best taxonomic expression of the morphology and evolutionary relationships of the Chlamydospermae is to treat them as a class of the Coniferophyta, coordinate with the class Coniferae.

If the several groups of gymnosperms and pteridophytes are treated as distinct divisions, then the angiosperms must also be treated as a division. Still admitting that the rank at which a taxonomic group is received is subject to unresolvable differences of opinion, I believe that the angiosperms would best be treated as a division, even if it had not become necessary to remove the coniferophytes from the remainder of the groups which have been associated as the Pteropsida. The absolutely sharp delimitation of the angiosperms, the uncertainties about their origin, and their dominant position in the land vegetation combine to mark them as a group fully worthy of divisional status.

The suggestions made by various authors that the angiosperms may be polyphyletic seem to be so contrary to the evidence that they do not merit a detailed refutation in this paper. Nor do I feel the need to review the abundant evidence that the Ranales sens. lat. are the most primitive existing group of angiosperms and that the carpel is truly a megasporophyll. It is perhaps worthwhile, however, to call attention to the suggestion of Bailey and Swamy (1951) that the primi-

tive position of the ovules is on the adaxial surface of the carpel. I concur in the present general belief that the ancestry of the angiosperms must be sought among the pteridosperms. Pteridosperms with the ovules on the upper surface of the magasporophyll are not numerous, but they apparently do exist. *Emplectopteris triangularis,* from Permian deposits in China (Halle, 1929), is an apparent example. The reasons for believing the angiosperms to be derived directly from the pteridosperms have been reviewed at some length by Takhtajan. (1958).

The advantages and disadvantages of dividing all angiosperms into monocotyledons and dicotyledons are too well known to require further discussion here. Admitting that a few families may prove to be misplaced, I concur with the majority opinion among taxonomists that the distinction between the two groups is a proper one. If the angiosperms are to be considered a division, then the monocotyledons and dicotyledons can appropriately be treated as classes.

The name Anthophyta, here adopted for the angiosperms alone, was originally proposed by Braun (1860) to apply to all seed plants. Most or all of the recent use of the name has been in the narrower sense of Bessey (1907), however, and I believe no serious confusion will result from this restriction. The only obvious alternative, Angiospermophyta, has also appeared in print but seems unnecessarily long.

CONCLUSION

In conclusion I wish to pay deserved tribute to two men for their outstanding contributions to the general system of plants during the twentieth century. Adolf Pascher's extensive and critical work on the algae, culminating in a general system (1931), is the foundation and inspiration for all modern algological systems. Charles E. Bessey is usually remembered for his well known work on the phylogeny and classification of angiosperms, especially as expressed in papers published in 1897 and 1915. In a less known synopsis of the plant kingdom (1907) he discerned with considerable accuracy the classification of embryophytes which the subsequent accumulation of evidence has made necessary. As with Mendel's peas, the scientific world was not yet ready, and I was surprised to find the present system so clearly foreshadowed in a paper more than half a century old.

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ECOLOGICAL EFFECTS OF FOREST FIRES

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Introduction 484
Effects of Fire on Soil 486
- Moisture Relations 486
- Texture 488
- Temperature During Burning 489
- Post-Fire Temperature 491
- Fertility 492
- Chemical Composition 494
  - Acidity 495
  - Organic Content 496
  - Nitrogen 497
  - Calcium 499
  - Phosphorus 500
  - Potassium 500
  - Minor Elements 500

Effect of Fire on Living Organisms 501
- Lower Plants 501
- Plant Diseases and Pests 503
- Bacteria 504
- Invertebrates 504
- Vertebrates 505
- Plant Succession 507
  - Grasses and other Herbs 508
  - Shrubs 510
  - Trees 511
    - Jack Pine 513
    - White Pine 514
    - Red Pine 514
    - Paper Birch 515
    - Aspen 515
    - Black Spruce 515
    - White Spruce 516

Summary 516
Literature Cited 517

INTRODUCTION

Fire has been a significant factor in determining the vegetation of North America for many centuries. This is evident from the numerous published references to telltale layers of charcoal in soil under forests, and to other evidences of past fires. This paper is an effort to bring together the literature concerning the extent of forest fires and their effects on soil and various forms of life.

Among the references to evidence of past fires is that of Soper (300) who discovered charcoal in different strata of peat in northern Minnesota, showing the periodic recurrence of fire in that region long before its settlement. From pollen analyses of peat from northern Idaho, Hansen (134) determined that severe and frequent fires inhibited the development of post-Pleistocene climax forests in that area. The importance of fire as a major natural factor contributing to forest succession was also stressed by Lee (201).

Evidence of pre-settlement fires is also inferred from the type and distribution of the present vegetation in many places. Maissurow (232) maintained that the typical northern-Wisconsin forest, consisting of a variety of uneven-aged, fire-tolerant hardwoods, developed between fires, and of even-aged, post-fire stands of conifers indicates that there have been fires in 95% of the virgin forest for at least five centuries. Chapman (59) believed that most of the old, even-aged white pine stands throughout the Lake States region originated on burned areas. Jones (172) also related the occurrence of even-aged stands throughout the north temperate zone to the occurrence of fire. Linteau (209) believed most of the extensive white pine stands north of the St. Lawrence to be the result of fire. In reviewing Land Office survey notes, early travellers' records and other evidence, Spurr (302, 303) was able to relate the pine forests of Itasca, Minnesota, to records of specific fires. Daubermire (78) also related the big pine woods of northern Minnesota to the occurrence of fire. Allen (7), however, believed fire to be completely deleterious to forest succession in the Lake States.

Lutz (221) described the extensive forest fires which have swept forested portions of Alaska in the past and cited references to similar, extensive fires in regions of Siberia and Alaska (241, 273). Rubner (281) believed that almost all of the forests of Finland showed evidence of past fires. Muller (252) found similar evidence in Bulgaria. Haig (129) presented as evidence of the importance of past fires in the United States, the fact that no other type of clearing occurred exten-

sively before white men, yet sub-climax associations are found everywhere in the country. Iverson (165), from pollen analysis, determined that considerable clearing of neolithic forests occurred by burning, and this was followed by weeds, then hazel and birch.

General observations have often indicated that fire has been selective in the species it favors. MacKenzie (230), in his 18th century explorations from Montreal, noted as curious the fact that where areas of pine, spruce and birch were destroyed by fire, only aspen were produced, even though none was there before the fire. Along the Alaskan Highway, in British Columbia, Hansen (133) ascribed the persistence of lodgepole pine and aspen to frequent fires, and the presence and increase of spruce to the reduction of fires in modern times. Oosting and Reed (261) cited fire as a major factor in determining the vegetation of the central Rockies, favoring lodgepole pine. Weaver (341, 342, 343) believed that fire has been a natural agent for thinning and improving ponderosa pine stands in the west for many years.

There are cases, however, where pre-settlement fires are believed responsible for the absence of forests. Asa Gray (124) and Stewart (308) believed that the grasslands or prairies of the Midwest were developed or increased because of annual fires. One of the major causes of the treeless barrens of Kentucky was probably the spring burning of grass by the Indians (277). In the western states, grasslands were frequently replaced by mesquite and chaparral as a result of fire (308).

In pre-settlement times, lightning was probably a major cause of fire (60), although the Indian practice of setting fires appears to have been very important (80, 120, 124, 216, 227, 308). The Indians used fire to improve visibility and travel in forests, to drive and trap game, to clear land for better pasturage and crops, to increase the berry supply, for communication, and to eliminate mosquitoes and flies.

Fire, then, has been a major factor in the ecology of forests and grasslands in North America. In many places throughout the country, large and profitable forests have developed following fire. In other places permanent scrub or grasslands developed. Under various conditions, prescribed or controlled burning is used to maintain or develop grassland, shrubland or forest. The following review of literature dealing with observations of the effects of fire on vegetation and soil is aimed at determining the extent and nature of findings concerning the factors involved in such effects.

The majority of the investigations of fire deal with the changes it

produces in the frequency or growth of certain species or groups of plants and animals. Most of the papers concerning possible mechanisms causing such biotic changes deal with fire's effect upon the soil. One must bear in mind, however, that the same principles do not necessarily apply in widely different regions and soil types, although it would appear that some general conclusions may be drawn from similar studies in widely separated areas.

EFFECTS OF FIRE ON SOIL

MOISTURE RELATIONS

The role of fire in increasing erosion and surface run-off, and in changing soil-moisture characteristics has been a subject of much concern in studies of the effects of burning on soils. It is logical to assume that, since fire often changes the vegetation and forest floor suddenly and drastically, by these actions, it also would change the reaction of the forest area to rainfall. However, the changes wrought naturally vary greatly with the conditions of the soil, forest floor, topography, region and type of soil.

Few workers disagree with the idea that extensive burning increases erosion, surface run-off and the possibility of flood on many sites. In Oklahoma, Elwell et al (97) reported that, over a nine-year period, water and soil losses were 12 to 31 times as great on burned as on unburned woodlots. In the pine region of the Sierras, run-off was 31 to 463 times as great and erosion was two to 239 times as great in burned areas (129). Increased erosion of wooded land has also been reported by many other workers (11, 25, 43, 67, 139, 181, 217, 220, 228, 247, 323, 325). Lutz (221) and Preble (274) reported the slumping-in of stream banks following fires, as a result of the destruction of steam bank vegetation.

On certain types of sites, however, erosion and run-off do not seem to be affected by burning. In California it has been reported that the burning of brush and woodland grazing lands apparently had no effect on run-off and erosion (2, 30, 331). Other studies of burned brush and grassland, however, have revealed increased erosion (90, 109, 256, 257, 285). Horton and Kraebel (157) reported increased erosion in brush plots in California following burning but stated that it is stopped if the proper pre-fire species re-invade the burned land. Brown (44) found that heavy rain in burned brushland in California brought down much debris and soil, whereas the run-off from unburned brushland was

essentially clear. Tedrow (320) emphasized that where the land is flat and the soil sandy, run-off is negligible, as is the case where controlled burning is usually applied. In the New Jersey pine barrens, fire did not affect the physical properties of the soil (49).

Erosion and run-off are the result of lower infiltration rates and decreased water absorption. Specific studies of these latter soil characteristics usually agree with the more general observations on erosion. In a study of infiltration rates on seven types of soil in Missouri, Arend (13) found burning reduced infiltration rates 38%, compared to an 18% reduction when litter was removed by raking. Similarly, Kittredge (178) found infiltration one-fourth as intense on land burned annually as on unburned land, and Meginnis (239) reported lower water absorption capacity for burned oak forests in Mississippi. Reduced water absorption as a result of burning has also been reported by other workers (16, 17, 164, 256, 257, 265, 333). However, Veihmeyer and Johnson (331) found infiltration rates of brushlands in California unimpaired by burning. Ferrell and Olson (107) reported that, in the western white pine area, burning had little or varying effects on infiltration rates.

A change in the reaction of soil to precipitation, with resultant erosion, may be caused by the alteration of the forest canopy, thereby changing the force and rate at which rainfall hits the ground (46). It might also be caused by a direct alteration of the soil texture, making it less permeable (164, 178, 284), or by reduction in frequency of soil fauna burrows and the channels produced by decay of roots.

A diminution of the actual moisture content of the upper layer of soil following fire is reported for different regions (22, 31, 91, 130, 147, 148, 151, 270, 284). Kivekas (179) found that a reduction in humus content after burning correlated with a decrease in the percent of moisture, and that this reduction continued for 50 years or more. However, at lower mineral soil levels, greater or unchanged moisture content was reported in several of these and other cases (91, 130, 270, 284, 319). A variety of methods for determining changes in moisture content have been used. In some of these reports (20, 31, 151) wilting point or moisture equivalent was used, while in others (91, 130, 270, 284) actual moisture content was determined. Blaisdell (31), studying burning of sagebrush and grasslands in the West, found that any reduction in moisture content, even in the top one-half inch of soil, was only temporary. No differences in moisture content between burned

and unburned plots were reported by Green (125), Wahlenburg et al (335), Wahlenburg (333) and Wicht (350) on various types of sites.

The importance of moisture-holding capacity in determining survival of forest trees was stressed by Kell (175) and Daubermire (79). Although Austin and Baisinger (16) reported that after burning there was a 33.7% reduction in the moisture-holding capacity in the top one-half inch of soil, many investigators agree that the moisture-holding or field capacity of soil is seldom affected by burning (22, 23, 151, 219, 307, 319). In the Douglas fir region, the field capacity of the duff and top 0.3 inch of soil was decreased with burning, but no change was noted below that (164). The presence of charcoal in sandy soil increased the moisture-holding capacity, while in clay soil, charcoal may have decreased it (317, 326).

The effect of these various changes in soil moisture relations upon the water table apparently vary greatly with different site conditions. Lutz (221) cited references (48, 128, 351) to indicate that where the ground water is close to the surface, destruction of forest by fire or other agencies will cause a rise in the water table, resulting in the production of swamp conditions, at least in Alaska. In Finland, Kolehmainen (180), however, did not believe that this occurred. He believed that the great numbers of plants which develop following a burn keep the water table normal, retaining the water where it will be available for later tree use. He further reported that in Sweden, burning has lowered the water table in some previously wet sites. This is because the unburned areas with thick moss cover do not freeze completely in the winter. Consequently, the spring surface thaw is absorbed into the ground and the water table is kept too high. When these areas are burned, however, they freeze in winter, the surface water runs off, and the water table is thus lowered to a more desirable level.

TEXTURE

The majority of studies indicate that most fires are not hot enough to produce a direct effect upon the texture of the soils, except where complete removal of duff and litter and subsequent exposure of mineral soil to rain result in puddling and baking of the surface (164, 178, 325, 221, 284). Garren (17), however, reported burned soil in southern states to have a more massive structure and to be less permeable to water. Similarly, Wahlenburg et al (335) reported that burned soil was up to five times as harder as unburned soil. Heyward (149) stated

that the absence of fire for a period as short as ten years in the longleaf pine forests results in a more porous, penetrable soil. Soils of sandy loam or heavier texture may exhibit fine crumb structure, and the humus layer will become mull-like. Kittredge (178) believed soil porosity is greatly reduced because of destruction of insects and other macroorganisms which channel the soil. Edwards (92) reported better tilth in soils in India as a result of high temperatures during slash burning, and Ehrenberg (93) ascribed similar findings to the fact that the heat of fire could make clay more friable. Stepanov (307) and Sreenivasan and Aurangabadkar (304) reported lumping and hardening of clay soils after burning, the result of colloidal aggregation.

TEMPERATURE DURING BURNING

Temperatures recorded during fires cover a wide range, as might be expected in fires at different seasons, weather conditions, type and quantity of fuel. Long recognized as among the hottest and most destructive are the heavy slash fires in the coniferous forests of the Pacific Northwest. Hoffman (155) found that in such fires of Douglas fir, cedar and hemlock, temperatures above the ground reached 850°F, while below 0.75 inch of duff, temperatures attained 120°F. The mineral soil under one and one-half inches of duff rose no higher than 60°F, while one inch below exposed mineral soil, temperatures reached 75°F. Isaac and Hopkins (164), in similar area, recorded temperatures of 1841°F above the forest floor and 608°F one inch below. Heyward (150), reporting soil temperatures during fires in the longleaf pine region, found that in the upper one-quarter inch of soil, temperatures reached 150° to 175°F for only two to four minutes. At the one-half inch depth, the rise in temperature was negligible, or in some cases reached 190°F. At one inch there was only a slight and insignificant rise. Elpatievsky et al (96) reported that the upper sandy mineral soil in large spruce and pine slash pile burns in Russia reached 500°F, and that the depth of heat penetration was greater in sand than in heavier soils. Beadle (22) found temperatures of sandy top soil in New South Wales varied from 178° to 415°F during fires, while at one inch depths, temperatures rose to a maximum of 153°F. Bentley and Fenner (28) recorded temperatures between 200° and 250°F at mineral soil surface when burning grassland with light litter, and temperatures below 200°F when the land was covered with heavy litter. Where brushland was burned, mineral soil surface temperatures rose to 350°F.

Uggla (330) reported little or no temperature rise in the humus layer of forest soil during burning because of the thermo-insulating properties of the moisture condensation barrier between litter and duff layers.

Investigations of the effects of such temperatures on soils and on subsequent plant life grown on the heated soils are contradictory. It has been reported (251, 290) that high temperatures induced chemical changes in the soil. They found the amount of soluble material beneficial to plant growth in extracts from heated soil was six to ten times greater than that from unheated soil. However, Pickering (272) reported that a non-acid, nitrogenous material harmful to plant growth was formed in soils heated without drying to between 60° and 150°C or higher. The greater quantity of this substance which inhibited seed germination was formed at 200°C, the amount diminishing at greater temperatures. Coults (73) found little change in soils heated to 250°C, but above that there was a 20% reduction in buffering capacity. Sreenivasan and Aurangabadkar (304) noted that the clay content of soils was reduced by heating, due to the aggregation of colloids.

Increased fertility of burned soils has been believed by some workers to be caused directly by the high temperatures during the fire, not by the addition of plant ash (131, 182, 304). Pickering (271, 272) however, reported that growth of broad-leaved species was less vigorous on heated soils, although growth of grasses was better. Seaver and Clark (290) found that heating soil to 194°F favored growth of oats, while temperatures above 248°F reduced growth. Wilson (355) found that heating soil to 96°C accelerated the growth and vigor of plants, while heating to 175°C delayed germination, retarded growth, and increased susceptibility to disease. Johnson (171) reported that heating soil increased germination by eliminating certain fungi pathogenic to seeds and seedlings. It is evident that the differences in the effect vary with the plant species used and the type of soil treated.

While Sampson (284) reports that most dry seeds are killed by exposure to temperatures of 250° to 300°F, for five minutes or more, seed of certain plant species may be stimulated to germination by heat. Among shrubs, Stone and Juhren (312) observed that germination of *Rhus* spp. seeds was 17 to 60 times as great after heating the soil containing the seeds because the high temperatures made the seed more water-permeable. Wright (357) found *Rhus* spp. germination increased by the action of temperatures up to 260°F. Germination of *Ceanothus* seeds was also stimulated by heat (275, 357), in some species by tem-

peratures as high as 280°F. *Rhamnus californica* increased in germination at temperatures up to 180°F (357). Wright (357) reported that heating the seeds of *Abies magnifica* to 180°F increased germination, the optimum being between 100 and 120°F. *Pinus ponderosa* showed slightly increased germination after exposure to temperatures up to 200°F, while *Pseudotsuga taxifolia* increased in germination rate only slightly at temperatures up to 160°F. No changes in germination with application of higher temperatures were detected for *Pinus contorta* and *P. lambertiana*. Stone (311) reported flowering of Brodianiae species to be stimulated by heat.

Among grasses, *Avena* species were stimulated by temperatures up to 220°F, while *Bromus* showed insignificant results (357).

POST-FIRE TEMPERATURE

Burning also affects the temperature of soil for some time after fire. This is partially the result of removing the insulating vegetation; more significantly, it is the result of increased light absorption by the blackened surface and by the presence of charcoal in the soils (36, 162, 221, 293, 326). Isaac (163) reported that at an air temperature of 89°F, the temperatures of surface yellow mineral soil rose to 125°F or higher, while in similar soil which had been charred, temperatures rose to 144°F. Hensel (140, 141) found that in burned over grasslands, at a one-inch depth, soil temperatures were 12 degrees higher maximum and two degrees higher minimum, while at three-inch depths, mixiumum and minimum temperatures were four to five degrees higher. Higher soil temperatures after burning were also reported by other workers (36, 135, 293, 335). Phillips (270) reported higher day but lower night temperatures in the top six inches of burned savanna soil in South Africa. In the Duke Forest, Pearse (264) found that similar, greater temperature extremes occurred on burned forest soil, and that these differences could be detected for at least five years after burning.

This change in temperature extremes affects various species differently. Hensel (141) believed that it would account for the earlier spring development of vegetation on burned plots. Shirley (293) found that it stimulated growth of aspen suckers. Often the increase in soil temperature is sufficient to kill very young tree seedlings and impede reforestation (36, 162, 225, 326). Undoubtedly other differences in vegetation and succession plant and animal life reported on burned lands might, if more fully investigated, be found related to these temperature differences.

FERTILITY

Observations on the effect of fire on soil productivity and fertility vary widely with region, soil and type of plant growth studied. Of more probable significance are those studies in which the change in fertility has been related to changes in specific soil substances or properties as reviewed in later sections. In many cases, however, a change in the plant yield of soil was observed after fire, but it was not identified with any specific soil constituent or property. Corson (71) noted that fire, by changing vegetation and fertility, interferes with the classification of soils into their adaptation to existing forest types.

Germination and very young tree seedling growth has some times been reported to be poorer on burned soil. In clarifying this, Fabricius (104), growing trees in pots of soil, found that covering the soil with ash reduced germination and early growth of all species studied. He noted, however, that the inhibition by ash was less on sandy soil than on loam. Heikinheimo (137) also carried out extensive tests in which ash was added to neutral sand and to peat, and the germination and growth of pine, spruce, birch and alder were studied. He recorded that the higher concentrations of ash hindered germination and growth of all four species, but that spruce and alder were more seriously affected. This, he believed, corresponded with the fact that spruce is often slow to return after fire. Schmidt (286), performing similar experiments with Scots pine, found that germination was improved by ash, although subsequent growth was reduced. Tryon (326) reported decreased germination of white pine seed in soil to which charcoal had been added. Perry (267) found growth of both white and red pine better on unburned soil. In France, Arnould (14) found that trees grew poorly for 100 years after fire on clay soil, and he believed this to be the result of compaction of the soil as a result of burning. Similar, shorter term results with redwood seedlings on clay soil were reported by Fritz (114).

Reduced growth of other plants is also reported. Without the presence of ash, heating soil resulted in less vigorous growth of most vegetation, according to Pickering (271, 272). While heating soil to 90°C was beneficial to growth of oats, heating to above 120°C was injurious to their growth. Thompson (322) reported burned soils less productive for oats and potatoes than unburned soils. Poor productivity of burned soil was also noted by other workers (97, 164, 279, 333, 356).

Alway (8) and Alway and McMiller (9) reported that burning had

no effect on productivity of crops on sandy loam in Minnesota, and Thompson (322) found that yields of hay and sunflower were similar on burned and unburned soil. From phytometer studies of pitch pine plantations in New Jersey, Lutz (220) found no consistent differences in fertility of unburned and burned soils, and, in the same area, Somes and Moorehead (299) reported no significant differences in growth of pine-oak stands as a result of burning. In South Africa no appreciable difference in soil fertility in brushlands could be detected after burning (23). In the southern Appalachians, fire had no significant effect on radial growth of shortleaf pine for two to 13 years after fire (169). Heyward and Barnette (152) found no marked change in soil fertility after burning in the longleaf pine region. Although productivity of steep slopes and rocky ledges is lessened by fire in Alaska (221), other sites do not seem to be affected in productivity.

On the other hand, reported stimulation of germination and growth of tree species has been reported frequently. Schmidt (286) reported Scots pine germination stimulated by application of wood ash to the soil, while in Madras, India, Laurie (194) reported that slash burning was beneficial to germination and height growth of most tree seedlings except teak. Kessel (176) also reported increased growth of tree seedlings around ash beds in Australia. In India height growth of tree seedlings was reported to be greater on burned than on unburned plots, especially the first year (126, 168).

The beneficial effect of burning on growth of herbaceous plants has also been cited frequently. While some of these reports may seem contradictory, to those reported above, it must be remembered that different species and soils are usually involved. Wahlenberg (333) reported that forage plants and corn grew better on burned soil in the longleaf pine region. Corn also produced better yields on burned soil in tropical Africa, according to Topham (324). The number and size of forage plants in the longleaf pine region was found by Greene (125) to be increased by prescribed burning. Fowells and Stephenson (110) reported a stimulation of plant growth after burning, but believed it to be very temporary. Blaisdell (31) found stimulation of grasses and herbs by fire to disappear after two to three years. Fertilizing action of ash on grasses was also reported by Curtis and Partch (76), together with an increase in grass flowering heads caused by the higher soil temperatures resulting from removal of the insulating cover of old litter. Kivekas (179) conducted experiments in which oats grown in

pots under greenhouse conditions yielded twice as much dry substance when grown on burned soil as when grown on unburned soil. Garren (117) also believed that burning increased growth of ground cover plants as a result of the return of minerals to the soil by way of ash. Beneficial effects of burning on plant growth were also reported briefly by other workers (94, 131, 143, 144, 182, 194, 202, 219, 293, 304, 332).

Conclusions on this subject are difficult, since soil productivity is dependent upon many factors, and fire may affect each of them differently. For example, erosion and run-off are generally increased by fire, with the resultant washing away of nutrients. However, under some conditions these harmful aspects may be more than compensated for by the stimulatory effect of ash on subsequent plant growth and on the growth of micro-organisms in the soil. These, in turn, replenish soil, both physically and chemically, and cut down on erosion and run-off.

CHEMICAL COMPOSITION

The sudden release to the soil via ash and subsequent rainfall of soluble mineral salts previously incorporated in plant tissue and usually returned very slowly by the decay processes is undoubtedly responsible for many of the changes in plant growth found on burned soils. Therefore, the temporary effect of burning may be helpful, but, since soil productivity depends on gradual mineralization and utilization of fallen litter, it would not be reasonable to expect continued and repeated burning to improve soil fertility (110, 117) unless this sudden, large supply of mineral nutrients were in some way immediately incorporated into the biological cycle before it could be leached away. Stephanov (307), working with Scots pine forest soils in Russia, and Katz (174), working on peat soils, and Burns (49) in the New Jersey pine barrens found that there was an increase in both water-soluble compounds of alkali and alkaline earth metals, sulfates and carbonates after burning. Haines (130), on the other hand, working on heathlands in England, found that two months after burning, the soluble salts in the soil were reduced by leaching 70% in the top two inches, and 86% below this. Heyward and Barnette (152), studying the effect of frequent fires on mineral soil in the longleaf pine regions, found the general chemical composition improved by burning, while Lutz (220), working in the New Jersey pitch pine region, found very little general change in soil chemistry. Improved soil fertility following fire has been reported in

many other areas (3, 4, 42, 98, 220, 288). More may be learned by investigations of the various elements separately. These are discussed in the following sections.

ACIDITY

It is reasonable to assume that the considerable amounts of ash left on the ground after burning will decrease the acidity, since ash is rich in alkaline material, and, according to Heikinheimo (137), 7% of the potassium carbonate and other similar salts will dissolve in cold water. However, no significant change in soil acidity as a result of burning was reported on various sites (22, 23, 220, 268, 332). Perry (226) reported a decrease in acidity as a result of burning in hardwood forests in Pennsylvania to be very temporary. The majority of the studies, however, indicate that fire usually decreases acidity (8, 16, 18, 21, 96, 99, 107, 117, 119, 125, 130, 152, 164, 179, 183, 212, 219, 236, 328, 330).

This change in acidity may vary with the depth and type of soil. Hess (143) found that burning lowered acidity of acid soils in Switzerland but had no effect on neutral soils. Alway and Rost (10) reported that, in Minnesota, acidity was lowered in the top three inches but unchanged below that after fire. Perry and Coover (268) found that the A horizon of frequently burned areas had the same pH as infrequently burned areas, but that there was a lower acidity in the B horizon, attributed to the leaching downward of ash materials.

The length of time these changes persist after fire differs. Eneroth (99) found that in Sweden, an increased pH of surface soil following burning lasted ten years. In English heaths, Haines (130) found that the lowered acidity of surface soils returned to normal in a few months after fire. Finn (108) burned organic material which had been placed on boxes of sandy and loamy soil, and found it resulted in a change to an alkaline condition which reverted to acid after one year.

The change in acidity, as previously mentioned, is usually believed to be caused by the presence of ash and by the resultant release of soluble mineral salts, especially those containing calcium (126). Subsequent leaching of these salts from the top layers results in eventual return of them to the original acidity. Reported differences in degree of acidity following burning and in the rate of return to normal indicate that the quality of the soil, type and amount of ash are important in determining the extent to which fire effects acidity. Eden (91) pointed out the pos-

sibility that the heat of fire may also destroy buffers, especially organic ones, as well as organic acids in the soil. Coults (73) reported a 20% reduction in buffering capacity of soils when heated to above 250°C. Munste (255) and Hessleman (145) found that after a burn, the alkaline materials from the ash neutralized free humic acid; when this happens, leaching of salts from the soil will be minimized. Svenhufruid (315) reported that up to 25% of the ammonia produced in burning can be absorbed if conditions are right.

ORGANIC CONTENT

The extent to which soil organic matter is destroyed by fire is very largely a factor of the fire intensity and temperature, the extent to which the organic matter is incorporated in the soil, and the type of pre-burn vegetation. Although Hosking (158) demonstrated that organic material heated to 100°C without combustion lost weight significantly, Heiberg (136) stated that fire does not affect organic material incorporated in the soil, probably because soil temperatures below the top inch of soil are not raised high enough during most fires.

Austin and Baisinger (16) found that the organic content of the top one-half inch of soil in western Oregon and Washington was reduced as much as 75.5% after fire. Two years later the organic content was still 50% below normal. Blaisdell (31) found a significant reduction in organic content in the top one-half inch of burned soil in sagebrush and grasslands, but the effect was temporary and disappeared after a few years. Isaac and Hopkins (164) found organic matter reduced one-third by burning in the top three inches, while below that the changes were insignificant. Always (8) stated that in a bad fire in Minnesota, the loss of organic matter ran from seven to 26 tons per acre in the surface layer, with little change below that. Barnette and Hester (18) compared soils burned annually for 42 years with unburned soil and found a loss of 2,088 pounds of organic matter per acre. In English heaths, Haines (130) found a loss of 60% of the organic matter in the top soil layers and an eight per cent reduction at lower levels. Minckler (243) reported fires can destroy as much as two feet of pure organic soil in spruce forests of the southern Appalachians. Ferrell and Olson (107) reported that the organic matter lost to burning in western white pine regions takes 50 years or more to be replaced. Diebold (85), in the Adirondacks, found the forest floor burned to an average depth of two inches. There are many other references to loss

of soil organic matter with burning (87, 97, 110, 179, 263, 266, 304, 325, 344), although Beard and Darby (23), Bruce (41) and Wicht (350) reported no significant loss in soil humus in their studies.

In Alaska, Lutz (221) found the loss of organic matter varied with the intensity and frequency of fires, but that deep burning to mineral soil, even in fires severe enough to kill all the trees, occurred on 30% to 40% of the total burned surface. Lovejoy (215) quoted an opinion of Dr. Marbut of the U.S. Soil Survey that any accumulation of forest debris is injurious to soil and forest growth, and that any method which removes it is good. Lovejoy holds, however, that there is insufficient evidence of the advantage of this to advocate extensive, controlled burning. Muller (252) also emphasized the beneficial importance of burning in reducing excessive raw humus, particularly in pine stands, although Lowdermilk (217) pointed out that the great reduction of forest litter caused by burning is a serious factor in the increase of erosion. Williamson (354) reported that annual burning of forests in Florida reduced organic content seriously, to a depth of four to five inches.

NITROGEN

One major factor controlling soil productivity is available nitrogen, and there is little doubt that in most cases fire affects the quantity available. At the same time, fire may cause changes in other soil conditions which in turn stimulate or inhibit the nitrification process carried on by soil and nodule bacteria and soil fungi. The activities of these organisms may obscure tests of the direct destruction or increase of soil nitrogen by fire, and this may be one of the reasons for contradictory reports in the literature.

Reports of lower nitrogen content following burning are frequent. In Florida, Barnette and Hester (18) reported an estimated annual loss of 27 pounds of nitrogen per acre when land was burned annually. In New Jersey, Lutz (220) found a slightly lower nitrogen content in frequently burned soils as compared with soils burned infrequently. A loss of nitrogen from the upper two inches of clay and loam soils after burning of wattle litter in Africa was reported by Osborn (263). Finn (108) reported loss of nitrogen by leaching in experiments in which sand and loam soils placed in boxes were covered with organic matter and burned. Losses of from 450 to 1,500 pounds of nitrogen per acre through losses in the surface cover were reported by Alway (8) in Minnesota. He found, however, little change in the upper mineral soil.

Austin and Baisinger (16) discovered a 67% loss of nitrogen in the top 12 inches with a 75% recovery of this loss two years later in burned soils in the Pacific Northwest. Lovejoy (215) cited Snyder's figure of a loss of 1,600 pounds of nitrogen per acre from forest fires in the northern Lake States region. Blaisdell (31), Elwell et al (9) and Wahlenberg (334) also reported losses of nitrogen from soil after burning. In Finland, Kivekas (179) found loss of ammonia from the top layer of soil with burning, but he believed this loss was much greater in brush fires than in sod burning because hotter fires oxidize organic material more rapidly with greater vaporization. Svenhufruid (315) reported that up to 25% of the ammonia formed during burning of peat can be absorbed by the soil after burning.

On the other hand, increased soil nitrogen as a result of burning is also reported frequently in the literature. Heyward and Barnette (152) reported higher total nitrogen after burning in soils of the longleaf region. Isaac and Hopkins (164) found no significant change in the nitrogen content of soils in the Douglas fir region after burning, and Chapman (58) reported similar results in loblolly pine stands. Garren (117) reported nitrogen increases in the southeastern states after burning, and Lunt (219) found higher total nitrogen after burning under red and white pine stands in the northeastern states. Tryon (326) found that coniferous charcoal in the soil increased the total nitrogen, but he detected no change in the amount of available nitrogen with such addition. Vlamis et al (332), conducting controlled fertility tests on soil from the ponderosa pine region, found that heavy burning increased nitrogen slightly. An increase in soil nitrogen after fire has been reported in many other areas (4, 10, 107, 117, 144, 220, 278, 284).

In discussing the effect of burning on the biological processes which restore available nitrogen to the soil in Finland, Kivekas (179) reported that, while ammonification is less, the nitrification process is greatly increased due to the effect of the changed pH on bacterial growth. Green (125), working with longleaf pine soils, found a large increase in growth of legumes after fire. These plants, he feels, were responsible for subsequent increases in nitrogen. Hesselman (144) also felt that burning increased soil nitrification and that such increases after burning could last from 12 to 25 years, depending on the type of soil and other conditions. He also found increased denitrification, oxidation of ammonia to nitrate, and reduction of peptones to ammonia—or increased bacterial activity in general. In Russia, Sushikna (314)

found that an increased nitrification rate was detectable two days after fire and lasted at least five years. Fowells and Stephenson (110) also reported increased nitrification by burning. In the Cameroon, control of the nitrogen cycle by burning, known as "ecoubage", is practiced in places where the nitrogen cycle is completed too rapidly (167). To conserve nitrogen, soil is allowed to remain fallow for two years. It is then allowed to grow up into brush, and the brush is burned. Three or four crops are then grown on the land, and the process is repeated. This burning is believed to "mobilize" the minerals, especially the nitrogen. Kivekas (179) found that the proportion of amino acid nitrogen to protein and amide nitrogen was much higher on burned land. He also found that the total nitrogen was reduced by burning, but not to a critical level.

CALCIUM

As would be expected, changes in soil calcium content correlate fairly closely with changes in acidity as a result of burning.

In the southeastern United States, significant increases in replacable calcium following burning were reported by Garren (117), Heyward and Barnette (152) and Barnette and Hester (18). Vlamis et al (332) reported similar increases in the ponderosa pine region as do Isaac and Hopkins (164) and Fowells and Stephenson (110) for soils of Douglas-fir regions. Hess (143) found that burning increased the calcium carbonate in acid soils in Switzerland but had little effect on the calcium content of neutral soils. Uggla (329) reported increased calcium after burning in Lapland. Lunt (219) reported an increase in exchangeable calcium under red and white pine forests after burning. Lutz (221) found a seven-fold increase in exchangeable calcium following fires in Alaska. Kivekas (179) found that after burning in Finland, there were significantly higher amounts of calcium in soil down to a depth of ten centimeters. Tryon (326) found that addition of charcoal to soil caused an increase in available calcium.

Austin and Baisinger (16), working with soils in the Pacific northwest, found that, as a result of mineral release from ash following burning, the soil calcium content increased as much as 830%, and that two years later it was still 327% as high as before burning. Wahlenberg et al (335) reported burned soil to have up to 100% more calcium than unburned soil in the longleaf pine region. Finn (108), however, in experimental studies, found that leaching after burning caused a loss of calcium in both sandy and loamy soils. Sreenivasan and Aurangabad-

kar (290) found that heat, in the absence of ash, lowered the amount of replaceable calcium.

PHOSPHORUS

In a complete fertility test using sandy loam and loam from the ponderosa pine region, Vlamis et al (332) found that on sandy loam there was a marked increase in available phosphorus following fire, while on loam there was no significant change. These different results were believed to be due to the fact that one type of soil tends to bind phosphorus and make it unavailable. Such binding may be the reason for other conflicting reports. Kivekas (179), in Finland, and Uggla (329, 330) in Sweden and Lapland reported an increase in available phosphorus as a result of burning, as did Lunt (219) and Lutz (220, 221) in the United States and Alaska. Austin and Baisinger (16) found, in the northwestern states, that soil phosphorus was twice as high after burning.

Tryon (326) reported increases of phosphorus with addition of charcoal to clay, loam and sand, while Lutz (221) observed no significant change in phosphorus content in pitch pine soils of New Jersey after burning, as did Isaac and Hopkins (164), Fowell and Stephenson (110) in the Douglas-fir region, and LeBlanc (199) in Quebec.

POTASSIUM

Available potassium was increased with burning in the Douglas-fir region (164), in Finland (179), Lapland (329) and in Alaska (221). Austin and Baisinger (16) reported potassium increase up to 166% following burning of soils in Oregon and Washington, with a drop to 112% two years later. Finn (108), however, stated that the leaching which follows most burning decreases soil potassium.

MINOR ELEMENTS

Worley (356), reporting on studies in New Zealand, believed that burning in general decreases soil fertility. Such elements as copper and manganese are usually brought to the surface very slowly by tree growth and are gradually returned to the humus at a rate at which the plants can utilize them. When burning occurs, these elements are released rapidly into the soil from the plant tissues as ash, and they are then allowed to leach out or down to the layers of soil unavailable to plant

roots, thus destroying the work of centuries in maintaining a delicate balance of these elements.

LeBlanc (199) pointed out the necessary balance of such minerals as manganese and magnesium in the maintenance of black spruce in Quebec. He stated that increases in manganese to very high levels is detrimental. However, excess manganese is made insoluble if calcium is added, so that the harmful effect of increased manganese is lessened after burning if calcium as well as manganese is released to the soil via the ash. Austin and Baisinger (16) reported a 337% increase in available magnesium following burning, with a return to normal in two years.

Very little work has been done on the content of the minor elements in ash and their effect on plant growth in burned-over areas. It is very possible that such investigations might prove very significant, since these elements, necessary in very small quantities and often toxic in large quantities, may be critical in plant succession.

EFFECT OF FIRE ON LIVING ORGANISMS

LOWER PLANTS

Special attention has been given to these lower forms of plant life in connection with forest fires. Since they are among the most frequent living components of the forest floor, their destruction or increase as a result of fire is important in the problem of water conservation and in competition or assistance to seedlings of higher plants.

Rainfall interception by mosses and lichens has been investigated in the New Jersey Pine Barrens, where Moull and Buell (240) found that mosses, especially the turf type, frequent after burns, can intercept and hold an average of 50% of the rainfall, while lichens intercept 25%. Together, these plants frequently cover 90% of burned land and are, therefore, important in determining whether rainfall reaches mineral soil. However, the authors do not believe that the mosses and lichens intercept as much water as does the thick, continuous layer of litter found on forested land not subjected to burning. Mosses are often completely destroyed by fire because they lack firm connection with the soil. Some species which form deep tufts may survive (327, 330).

Kujala (185) believed fire to be more destructive of lichens and mosses than it is of higher plants. Buell and Cantlon (45), however, in the New Jersey Pine Barrens, found that burning stimulated growth

of mosses and lichens greatly, and that increased light caused by removing the upper vegetation favored lichens over mosses. Lutz (221) believed that most moss reproduction following fire was vegetative, coming from fragments which survived fire instead of from spores. Hustich (160) believed that in northeastern Canada, recovery of the lichen cover following fire required at least 40 years. Lewis (207) and Lewis et al (208) did not believe that fire was a critical factor in the retrogression of sphagnum or muskeg areas in Alberta, while Stallard (306) stated that in northern Minnesota, fire very frequently causes a shift from sphagnum to grass in bog land.

Smith (298) believed that, as a seedbed for white pine, *Polytrichum* spp. and similar mosses and the moist mineral soil below them make better conditions than exposed, dry mineral soil or forest litter. This is partially because of the insulation furnished by the moss, but more significantly because seedling roots can penetrate moss and get into the mineral soil more successfully than they can penetrate litter.

In those cases where they have been studied, certain moss and lichen species have been found characteristic of burned areas, and typical post-fire succession occurs which corresponds to the succession found among higher plants (1, 74, 160, 174, 185, 285, 296). *Ceratodon purpureus, Funaria hygrometrica* and *Marchantia polymorpha* (122, 123, 334) are typical fire followers in many widely scattered regions, as are *Pohlia* spp. and *Polytrichum* spp. Among lichens, *Biatora, Baeomyces* and *Cladonia* species are frequently mentioned.

The fungus flora of the forest floor also changes with burning. In the Transvaal, Cohen (65) found that burning and light grazing stimulated the production of fungi and favored active spore production. Sarvas (285, 289) also noted an increase in fungi resulting from fire, especially those belonging to *Peziza* (Discomycetae). Moser (249) found that the Agaricaceae and Discomycetae were increased most markedly on burned soils. In comparing different kinds of burned soils, the difference in fungi was largely quantitative and not qualitative, and the differences occurred with different intensity of burning. A characteristic succession of fungi after fire was also noted, that is, the fungus flora differed in newly burned land as compared with land burned further in the past. Tryon (326) found the presence of charcoal in the soil did not appreciably affect the fungi present. No detailed studies of the effect of fire on the smaller, non-fleshy fungi were available.

PLANT DISEASES AND PESTS

In some cases fire may aid in the control of plant diseases. Muller (252) pointed out the value of fire in purging the forest of insect and fungus enemies, and in restoring vigorous, fast growing species. Siggers (295) reported that a single winter fire may almost eliminate brown needle spot, caused by *Septoria acicola,* on longleaf pine, although the disease reappears the second season, and by the third post-fire year is as frequent as before the burn. The reduction of disease for at least two years, however, results in a greater foliage retention and better seedling development. Chapman (55) and Garren (119) also reported the use of fire in the control of *Septoria* on longleaf pine.

Markim (234) found that burning controlled red leaf *(Exobasidium)* disease of blueberries and blueberry leaf spot *(Septoria).* Cantlon and Buell (52) presented the idea that fire may reduce the occurrence of some virus diseases by destroying the insect vectors, notably leaf hoppers. LeBarron (197) and Weir (347) reported that fire effectively controls dwarf mistletoe which can be spread only by seeds from infected, living host plants (spruce). Haig (129) mentioned the use of fire to control bark beetles, nectria canker and other forest pests. Muller (252) also cited the use of fire in Bulgaria to control several fungus and insect enemies.

In some cases, however, fire may favor the increase of disease by producing thick stands of the host plant and thereby induce multiplication and spread of the pathogen. Demaree and Wilcox (82) believed this to be the case with certain leaf diseases of blueberries, such as powdery mildew *(Microsphaera alni)* and a rust *(Pucciniastrum myrtilli).* Davis and Klehm (81) reported increase of *Ribes* after burning unless the *Ribes* was eliminated by a second burn or other eradication methods. This, of course, would affect the spread of white pine blister rust. Schmitz and Jackson (287) reported that, in Minnesota, fire scars on aspen are the main port of entry for *Fomes ignarius,* the pathogen causing heart rot. Richmond and Lejeune (280) reported a large increase in wood boring insects in fire-killed white spruce in northern Saskatchewan. Kirkpatrick (177) believed that, by eliminating the proper habitat for birds which prey on insects, many insect pests are allowed to thrive after burns. The weakened or dead trees on the burned area may provide a medium on which fungi and insects thrive. Basham (19) reported extensive growth of *Fomes* spp., causing heart rot, on fire-damaged jack, red and white pine. Richmond

and LeJeune (280) reported an increase of wood-boring insects in burned white spruce stands in northern Saskatchewan. Schmitz and Jackson (287) found that fire scars on aspen are the chief portals of entry for heart rot in that species.

Wilson (336) reported that heating soil to 175°C resulted in increased susceptibility to disease on host plants later grown on this soil.

BACTERIA

A change in soil bacterial population with burning would be expected, since burning frequently raises the soil pH, a factor critical in bacterial growth. Indirect evidence of an increase in bacteria is contained in the reports described earlier, that nitrification—a process largely dependent upon soil bacteria—often increases after fires.

On the Malay Peninsula, Corbet (70) studied the effects of felling and burning virgin timber and found that the number of microorganisms rose immediately after fire but fell to the preburn level one week later and remained there for nine months or longer. In Switzerland, Dugelli (88) discovered that mixing ash with mineral soil did not significantly change the number of bacteria, and Wahlenberg et al (335), in the long leafpine area, were not aware of any significant increase in number of bacteria per acre after burning. Similarly, Jacques (167) reported that, in the Cameroon, burning did not disturb the microflora. Hall (131) found that if soil was heated for one hour to 100°C, there was an initial decrease in bacterial count followed shortly by a significant increase. Destruction of microorganisms in the top soil layers was cited by Kivekas (179) and Fritz (114). Hesselman (144) believed that charcoal in soil favored growth of bacteria. He stressed the fact that burning causes a complete change in bacterial flora. Tryon (326), however, claimed that addition of charcoal to soil did not appreciably change the abundance of bacteria. Isaac and Hopkins (164) asserted that, in the Douglas-fir region, slash burning and the subsequent calcium release favored growth of *Azotobacter*, an important nitrogen fixing genus. Lutz (220) also believed that *Azotobacter* and *Clostridium* increased after fire, as well as the nodule bacteria in wild legume roots.

INVERTEBRATES

In studying the soil microfauna in burned veld in South Africa, Coults (73) stated that the majority of the population in the top inch of soil survived ordinary burning processes. Heyward (149) reported

that excluding fire from the longleaf pine forest for as short a time as ten years resulted in a more active soil fauna. Heyward and Tissot (153) determined the microfaunal population of unburned A_0 horizons to be five times as great as that of burned soil, while the top two inches of unburned mineral soil had 11 times larger population than burned soil. In general, the species or organisms in the two areas were the same, although fire significantly reduced the proportion of earthworms to other organisms. In the Duke Forest, earthworms, centipedes, millipedes and ants were significantly reduced in number after burning (264). Of ecological significance also was the fact that important soil nesting pollinators, such as bumble bees, were also seriously reduced in number. Burning, however, was not as detrimental to soil fauna as mechanical removal of litter by raking.

VERTEBRATES

Damage to wildlife has been much publicized (e.g., 89, 125, 204). Animals, in their dependence on vegetation for food and cover, are variously affected by fire. Deer, for example, are usually associated with post-fire vegetation. Leopold (206) pointed out that deer are most frequently found on the sub-climax forest characteristic of burned-over areas, and that a climax forest does not favor their existence. Leopold, Sowls and Spencer (205) pointed out that fire stimulates the production of browse and results in an increase in the deer population. Ten years after fire, if there is no further burning or logging, tree crowns close in, reduce browse supply and result in a lowered carrying capacity and a deer population too large to be supported by this reduced food supply. Lay (195) reported that in east Texas prescribed burning did not damage habitat for deer and would improve the quantity and quality of deer forage, while Dasman (77) emphasized that such improvement or possible damage to deer forage depends on a number of area conditions.

Lloyd (214) emphasized the association between the quick growth of deciduous species which sprout abundantly after fire and the abundance of deer, in contrast to the almost complete lack of wildlife in unbroken forests. He pointed out that fires favor deer and grouse, although some other species disappear with fire—as in the case of caribou in northern Ontario. He stressed the complexity of the problems of wildlife and fire, and the fact that each case must be considered individually. For example, fire rarely results in a significant direct loss of wildlife because

the fires are usually too small to destroy an appreciable number of individuals. However, there are cases where the destruction of individual nests may be important to the survival of a rare or local species, for example, the heath hen which was exterminated by scrub fires on Martha's Vineyard. Fires increased the browse and were beneficial to herds of moose on Isle Royal and in Alaska (6,301).

Lloyd (214) further pointed out that some birds find ideal nesting conditions in fresh burns. The house wren and bluebird for example, are typical fire-followers. Other species follow a few years later. Stoddard (309) found fire very beneficial in the management of quail in the southeastern states. Kirkpatrick (177), however, reported that spring burning of marsh areas in Wisconsin completely disrupted the breeding season of a variety of low-nesting birds, and that they were driven out of the burned areas, thus allowing insect pests to thrive. Leopold (204) pointed out that the greatest damage to bird life is done by spring and early summer fires which destroy eggs and young, and ruin cover and food.

In Missouri, Terril and Crawford (321) reported that fires which follow logging eliminate squirrels from an area for ten to 25 years, unless a sufficient number of den boxes are immediately placed in the area. Nagel (258) reported that flood and lack of food which limit development of the beaver population in Missouri are due, in part, to forest fires. Destruction of fur-bearing animals has been emphasized by Lutz (221), Brabant (37) and Seton (291). Michaelis (240) reported that rodents were completely eliminated from a young hardwood plantation in Pennsylvania by fire. Destruction of small mammals by fire is also stressed by Gabrielson (115). Cook (68) reported that lack of cover following burning is the restricting factor in reducing mouse populations, especially for *Microtus* which requires one year mulchl for runways. He found shifts in species corresponding with fire—induced changes in vegetation from grassland to seed-produced annuals or from brush to grass. Similary, in the longleaf pine region, rodent damage can be reduced by prescribed burning which destroys grass cover necessary for seedling destroying rat species (238).

Leopold (204) and Kirkpatrick 177 have reported that, because of the wash of ash into lakes and streams after fire, fish are frequently killed.

PLANT SUCCESSION

Very few generalizations can be derived from the literature concerning plant succession following fire, since so many conditions in addition to the actual burning come into play as factors in the process. Typical post-fire sequences are inferred in many of the references, and characteristic fire-following plants are mentioned frequently for various regions. Lutz (221) stressed the necessity for evaluating quantity of seed produced, adaptations for dispersal, and efficiency of dispersing agents as well as such site factors as light and exposure of mineral soil.

Buell and Cantlon (45) believed that fire was a factor quite secondary to climate in controlling plant succession and the establishment of maple-basswood after pine-oak, common on the prairie in northwestern Minnesota, although Buell and Niering (47) recognized the destruction of pine forests in northeastern Minnesota as a major factor in the establishment of fir-spruce-birch forests. In Alaska fire has been more important than soil types and superficial geology in the establishment of forest patterns (276). In Finland, Sarvas (285) believed the appearance and subsequent spread of various plants on burned areas was dependent on the previous forest type. However, this does not mean that post-fire vegetation would necessarily develop into the same forest type or even the same major vegetational group as was present before the fire, at least not for many years.

In Switzerland, Ludi (218) reported that in a *Pinus-Larix-Picea* forest, the flowering plants which appeared after fires were mostly ones which were present in the pre-burn vegetation. However, he predicted that a long period would elapse before willow, birch, larch and finally pine would return. In the loblolly pine region, Oosting (260) reported that changes in herb and shrub vegetation following burning were very temporary. Growth of sapling or larger pines was slightly reduced, while that of lower strata hardwoods, especially oak and hickory, was increased. New reproduction of pines, however, was good and could compete successfully with hardwoods.[5] In following the revegetation of a burn in British Columbia, McMinn (229) found that the succession took varied courses and progressed at different rates because of pre-burn vegetation, edaphic conditions, available seed and microclimatic variations. LeBrun (200) believed the savannahs of central and eastern Africa to be of fire origin, woody species appearing only in the long absence of fire.

In Nova Scotia, on a burn of spruce-birch-oak-maple sites, Martin

(237) found that the herds and shrubs appearing during the first two years were all of sucker origin or developed from seeds which survived in the soil. However, Kujala (184, 185) divided the fire followers into four classes: *a*) plants provided with underground reproductive structures which survive the fire and produce sprouts; *b*) plants with seed which survive the fire in soil; *c*) plants with wind-disseminated seed; *d*) plants with a combination of fire-surviving or wind disseminated seed and vegetative sprouting.

GRASSES AND OTHER HERBS

A vigorous growth of herbs characteristically succeeds fire in many places. This lush, rapid growth may be related to the fertilizing action of mineral nutrients released by the ash, as discussed in earlier sections. In British Columbia, McMinn (229) reported that after a burn, bracken fern reached sufficient density to retard all forest regeneration. Martin (237), studying early development of plants following fire in Nova Scotia, also reported vigorous survival of bracken as the dominant plant because of its underground root system which survived the fire. Curtis and Partch (75) reported that after fire on prairie land, herbs increased markedly with the destruction of grasses and the increase of bare ground. Garren (117) found in the slash pine region that burning of both forest and open range resulted in great increases of herb growth, including wild legumes. Similar increases in legumes were also reported by Greene (125) in the longleaf pine region. Blaisdell (31), working on sagebrush land, found that herbs increased two to three times after fire, but he predicted the increase would be short-lived. Buell and Cantlon (46), in the New Jersey pine barrens, found burning to be followed by an increase in herbs, but they believed this increase to be caused mostly by an increase in light, since similar increases also occur after cutting. Hesselman (144) reported that the increase in the well known fire follower, *Epilobium,* is probably due to an increase in nitrogen in the soil, since this species is known to accumulate large quantities of nitrogen in its tissues. In New Zealand, Dick (83) found frequent 19th century burning of mountain beech resulted in a vegetation consisting largely of grasses. Mark (233) concluded that fire was not important in the maintenance of grass balds in the southern Appalachians, while Clements (63) believed fire to be crucial in their development.

Lutz (221) believed that, although many fire-following herbs reproduce vegetatively, the majority of species which invade burned areas

have wind disseminated seed. As with shrubs, Kujala (185) and Petterson (269) held that fleshy-fruited species are rare on burned over lands because of the scarcity of animals necessary for their dissemination. These workers, however, apparently overlooked the possibility of dissemination by fire-following birds (214). Ahlgren (3, 4) found the majority of plants appearing on burned land in northeastern Minnesota to be of vegetative origin. Seed-reproducing plants on the burns were usually not found on nearby, unburned land. Many produced animal- or wind-disseminated seed.

On lightly used range in California, Hervey (142) and Sweeney (316) found that fire increased herbs and decreased grasses, although on heavily grazed land, burning had little effect on the proportions of herbs to grasses. Dix and Butler (86) stressed that the responses of grasses to fire varies markedly with species and that, therefore, each species requires special study. Oosting (260) reported that in the loblolly pine region, any change in herb population following fire is very temporary. Pickering (272) reported that grass grew more vigorously on heated soil than on unheated soil; while other herbs grew less vigorously.

On certain types of land, a stimulation in the production of grasses has been noted after burning. In western regions, with an elevation of 1,600 to 4,000 feet, burning did not injure perennial grasses and seemed to encourage their spread by removing the dense pine needle mats and killing back the competing shrubs, according to Weaver (341). Stahelm (305) also reported that in the Rocky Mountain coniferous forests, burning seemed to cause an increase in grasses and other herbs. In studying western sagebrush, Blaisdell (31) found the total yield of grasses to be increased for three years following fire, but this increase was not believed to be permanent.

Burning as a stimulant to flower and seed production in several species of grass was reported by Cornelius (72) and Burton (50). For several perennial grasses, Curtis and Partch (76) reported that removal of old litter either by fire or clipping increased flower production six times because the removal of the old insulation permitted earlier growth and build-up of food reserves before flowering time. They also found that there was further growth stimulation which could be attributed to the fertilizing action of ash.

Stallard (306) reported that in upland areas in northern Minnesota, repeated burning frequently may result in the production of a grass

stage, while in bogs a reed or rush stage is produced. Either of these may delay the development of forest.

In bluegrass prairie land, when annual or biennial prescribed burning was done in March, May or October, the density of the bluegrass sod was reduced to one fifth the original after six years of burning, although the fruiting stems increased in number (75). Hervey (142) reported that on grazing land, fire had little effect on the proportion of grasses to herbs if the land was heavily grazed. On ungrazed or lightly grazed land, however, fire decreased grasses. Lemon (203), in studying post-fire succession in longleaf and slash pine areas, recognized bulky, perennial grasses with underground basal meristems which survive fire as one of the major plant types to appear immediately after fire.

In New Zealand, Sewell (292) attributed the deterioration of montane tussock type grassland, in part, to burning. He believed that burning killed tussocks and removed the protection of old leaves. After burning, two or more years were required to reproduce the proper microclimate for seed germination.

SHRUBS

Shrubs are generally believed to increase prolifically after fire. Lynton (223, 224) found this to be especially true after repeated fires on poor soils and believed the presence of such plants limited tree reproduction. Lutz (221) pointed out that because of their low stature and small stems, shrubs are very liable to destruction by fire, although they resprout vigorously. According to Petterson (269) and Kujala (185), shrubs with flushy or pulpy fruit regenerate slowly after fire, since they are dependent upon animals which are scarce in burned areas for their dispersal. Uggla (329), however, believed that many seeds survive the fire in the soil. Wind-disseminated plants such as willow come in rapidly. This, however, does not hold true for many shrubs which reproduce by suckering as, for example, *Vaccinium* (1, 113, 179, 285, 328).

Increase in shrubs may be due, in part, to the fact that heat stimulates the germination of seeds of some shrub species, as reported in previous sections (186, 275, 313, 349). Part of the increase in growth of shrubs may be caused by the increase in available nitrates and other minerals. Hesselman (144) and Uggla (330) reported that *Rubus idaeus*, a common fire follower, requires and accumulates very large quantities of nitrates in its tissues. McMinn (229), reporting on a

burn in British Columbia, found dense tangles of *Rubus spectabilis* which attained sufficient density to retard regeneration of the forest. In the redwood region, Fritz (114) reported that controlled burning of logged-over land could increase the fire hazard by producing an extremely heavy mass of shrubs. In the Colorado headwaters area, Ives (166) found that brush reaches its maximum density 25 years after the burn.

A change in the relative frequencies of various species of shrubs following fire has also been reported. Cantlon and Buell (52) and Buell and Cantlon (46) reported that in New Jersey, the frequency of *Gaylussacia* decreased while *Vaccinium* increased rapidly. Horton and Kraebel (157) also reported changes in the relative abundance of various species of chaparral shrubs in southern California following burning. Oosting (260), however, reported that burns in loblolly pine forests produced very temporary changes in shrub frequency, except for a definite and long-lasting increase in Virginia creeper and poison ivy.

TREES

Because of the structural and physiological adaptations among them, the effects of fire vary with different species. Therefore, each must be considered separately. This review will treat the effect of fire on species characteristic of the northern boreal forest which have not been extensively subjected to prescribed burning as a management practice. The practical application of fire in the management of southern and western species has been under study for many years and will not be included here (12, 15, 16, 20, 33, 54, 56, 57, 58, 60, 66, 117, 127, 173, 193, 195, 247, 336, 338, 339, 340, 341, 342, 344, 345). The application of fire by prescribed burning in northern forests has not been extensive except in Europe (180, 297, 299).

In considering the effect of fire on a given species, it is necessary to consider the direct effect on the tree itself at different ages from seed to maturity, and the more indirect effect of fire in creating a beneficial or harmful environment for the growth of the species at different ages. Optimum conditions vary not only with species but also with age. Wright (357), for example, has shown that exposure of various conifer seeds to high temperatures for short periods can stimulate germination in some cases—i.e., *Abies magnifica* and *Pinus ponderosa*—but does not effect germination in others—i.e., *Pinus contorta* and *P. lambertiana*. Borman (35), studying *Pinus taeda*, found that young seed-

lings achieve maximum photosynthesis rates in low light intensity. However, after secondary needles mature, the maximum photosynthetic rate is achieved in relatively high light intensity. Therefore, this species, at least, requires different conditions for optimum growth at different ages.

Early stages of conifer growth are generally believed to be favored on burned land, mainly because seedbed conditions are improved (54, 57, 129, 210). Little and Moore (212, 213) reported that the ecological effect of burning on seedbed conditions for most conifers is mainly physical, the result of the removal of the forest floor, thus favoring survival of most conifer seedlings over that of deciduous species. The reason for the basic difference lies in the initial root system. In pines, this root is only about one inch long, with about the same length of stem. In many hardwoods, however, the fleshy cotyledons permit development of a five- to six-inch root system before the first leaves begin to function, on stems two to three inches tall. The roots of hardwoods thus are able to penetrate unburned, deep litter to mineral soil before the leaves have an increased water demand, while those of pines are shallow and can reach mineral soil before drying out only if the litter has been at least partially removed, as by burning. Similar explanation was given by Farrar and Fraser (105) for results of laboratory experiments which demonstrated that humus did not contain a chemical which inhibited germination, and that if jack pine seeds were sown on deep humus and were watered thoroughly, good germination was obtained. Bonner (34) found that pure stands of hardwoods were very infrequent after fire in northern Ontario. On swamps, spruce and larch seeded in, while on high ground spruce and mixed hardwoods appeared. While much of this seed is dispersed after fire, a significant amount is present in the soil prior to fire (154). Buell and Borman (44) found, in northern Minnesota, that in the absence of fire basswood, fir and black ash replaced fire-following paper birch and white pine.

Haig (129) believed that burning was of great value in exposing mineral soil for a seed bed. The exposed mineral soil dries more slowly, fluctuates less in moisture content and temperature than the humus layer, and thus is more favorable to seedling growth. Although the abundant ash released may be of nutritional value, he believed this to be of secondary importance. Frazer (111) pointed out that forest trees having low moisture requirements are most frequent fire followers.

Tryon (326) and Isaac (163) reported that seed bed conditions could be made poor by addition of charcoal which increases soil temperature sufficiently that it may kill seedlings. However, Retan (277) noted that under nursery conditions, the addition of charcoal to heavy clay soil produced a marked improvement in coniferous seedling growth. Ooyama (262) stated that extracts of unburned litter inhibited seed germination and seedling growth of some species, especially the pines. Gemmer et al (118) asserted that ash stimulated germination but inhibited radicle penetration of longleaf pine seedlings.

Burning as a method of slash disposal in order to eliminate the hazard of wildfires is frequently proposed (187, 192, 211, 222, 226, 235, 246, 254, 342, 343, 344, 345, 352, 353 also 33, 120, 132, 358), although it is considered costly and dangerous by others (61, 192).

JACK PINE. Of the northern species, jack pine is most often recognized as a frequent post-fire species (175, 199, 232 and others). The ecological adaptation to fire of the serotinous cones has been pointed out (60, 4, 100, 101, 197, 198). Seed remains viable within the cone for many years, and the cones are opened by heat. Consequently, when a jack pine forest burns, or when the slash in a cut-over area is burned, seed is readily available. However, Watson (337) believed that proper restocking could occur after fire only if there were at least 75 seed trees left per acre. On many sites, however, jack pine reproduction is prolific and many fewer seed trees are necessary. Eyre (101) also pointed out that a large number of seed trees is necessary for restocking jack pine stands after burning, and that the seed is often killed by fire. Eyre emphasized the possibility that seedlings which come up immediately after late summer and autumn fires will not be strong enough to survive the winter. Johnson (170) believed that all methods of slash disposal, including fire, were detrimental to jack pine reproduction. The Lake States Experiment Station reported (189, 190) that spring fires frequently do not damage merchantable trees but are responsible for lack of reproduction in older stands. Mitchell (244) reported damage to older trees and the elimination of smaller ones.

Requirements for germination and young seedling growth are often met ideally by post-fire conditions. The exposure of mineral soil as a seedbed is advantageous (4, 62, 91, 113) because it is necessary for the young roots to reach a more steady supply of moisture than exists in forest litter and humus. Partial shade is required for good germination (60, 112, 113), and this is usually furnished by the characteristic

lush herbaceous growth the first year following fire[4]. Direct sunlight is advantageous for later seedling growth. This condition is usually present in the opening created by fire, once the seedlings rise above the herb-shrub layer. Bensend (27) found that jack pine seedlings require 200 to 250 ppm nitrogen for optimum seedling growth. Since fire is frequently reported to release nitrogen into the soil, this condition may also be met by fire.

There are frequent reports (102, 190) that spring fires were particularly destructive of seedlings and smaller jack pine trees but caused little damage to merchantable timber. Summer fires, since they are usually hotter, crown and burn deeper, did considerable damage to larger trees. Damage to trees of all size classes at any season was great enough, however, that burning to control brush, etc., in the productive stands could not be recommended. Rudolph et al (282) suggested that the distribution, in Minnesota, of jack pine having the fire-favored serotinous cones may have been influenced by the state's fire history.

WHITE PINE. Many worker have recognized that the existing white pine stands very frequently occur on burned-over land (39, 60, 64, 159, 196, 221, 245), although Cary (53) pointed out that fire is not necessary for the establishment of white pine on all sites. Kell (175) reported that white pine occurs as a pioneer on clay-loam sites after fire, while jack and red pine invade sandier, drier soils. Perry (267) found that white pine seed germinated best on burned soils, although subsequent growth was better on unburned soil. However, Lunt (219) reported that burning increased height growth by 8.1%, and volume growth by 18.8%, probably because of the higher pH, nitrogen, potassium and calcium concentrations in the topsoil. Cary (53) and Chapman (59) pointed out that white pine frequently comes in after blowdowns as well as after fires, so that the effect of fire may be largely one of opening an area to light. Maissurow (231) also held this view, since he maintained that white pine would reestablish after logging without burning if the areas were logged properly with due respect for good seed years.

RED PINE. Published references to the effect of fire on red pine are few, and it would appear that knowledge of fire and this species is very incomplete. Lunt (219) found fire stimulated height and volume growth of both red and white pine. Kell (175) observed that in Itasca Park, Minnesota, red pine was a post-fire pioneer on coarse soils, along with jack pine. Perry (267) reported that red pine seedlings grew better on

unburned soil. Maissurow (232) believed that many good, mature red pine stands existing today are the result of fire. Ahlgren (4) reported good growth and survival of planted red pine on burned-over land. Eyre and Zehngraf (103) believed fire could be useful and not damaging in slash dispersed after red pine cutting.

PAPER BIRCH. The best paper birch stands almost always occur on burned or cutover land, according to Betts (29), Weaver and Clements (346) and Gibson (119). In Alaska, Lutz (221) reported that seedlings of birch thrived on burned land, since they require mineral soil and full sunlight. He also found that relatively few mature trees survived even quick fires, although sprouting in young stands was very vigorous, less frequent in older stands. On the whole, he believed that seedling growth was much more important than sprouting in the re-establishment of birch following fire. Heikinheimo (138) found that birch seeds and seedlings were less harmfully affected by the presence of ash in the soil than were those of spruce and alder. Ahlgren (4) reported best seedling germination in northeastern Minnesota on burned land in low-lying sites, two to three years after fire, with vigorous vegetative sprouting the first post-fire growing season.

ASPEN. Aspen is generally recognized as a fire type. Shirley (294) and Breitung (38) pointed out the difficulty in the conversion of fire-perpetuated aspen stands to more desirable pine and spruce stands. They believed frequent fires to be one of the main reasons while large acreages in Canada and the Lake States remain covered with unproductive aspen stands. The Lake States Forest Experiment Station (188) found that in aspen stands which were cut and planted with pine and spruce, burning stimulated both the production and height growth of suckers to such an extent that they would compete with planted stock. Stimulation of sucker growth was also reported by Lutz (221) and Shirley, (293) who believed it to be caused by increased heat absorption by the fire-blackened surface. Uggla (328) found that in Lapland aspen seed germination and growth was very vigorous on burned land. Ahlgren (4) found germination best on moist seed beds two to three years after fire, with vegetative sprouting the first year. Stoeckler (310) reported that repeated burning was bad for aspen site index.

BLACK SPRUCE. Although mature trees are easily killed by fire (221), black spruce is quick to re-establish on an area subsequent to fire (26, 32, 156, 196, 221, 253). Lebarron (196) pointed out that prompt reproduction following fire is the result of serotinous cones which retain

viable seed for up to three years and open when exposed to heat. Trees begin producing seed at an early age and do so frequently, so that a good seed supply is almost always readily available in a burned stand. Fire also exposes peat and cuts down on competition of cedar and tamarack. LeBarron (197), Bellefeuille (26) and Millar (242) all reported that the best quality stands of black spruce occur on burned areas, so fire must be beneficial not only to initial reproduction but also to subsequent growth. Ahlgren (4) discovered good seedling growth after burns where the fire had not been sufficiently intense to destroy the cones in the tallest trees. Dickson (84) found spot seeding to be necessary to insure good re-establishment of black spruce following fire in Newfoundland.

WHITE SPRUCE. Lutz (221), observing forests in Alaska, reported that white spruce was very susceptible to fire. It was slow to return to burned areas because it seeded sparsely and not at an early age, in contrast to black spruce. Also, fire quickly destroyed the seed available in the nonserotinous cones so that it had to be blown in from unburned areas if it was to re-establish naturally. Heikinheimo (137) reported that ash inhibits germination and seedling growth. Saari (283) also reported that the species is easily damaged by fire. Holman and Parker (156) found white spruce to reproduce well after severe, late summer and early fall fires, but not after spring and early summer fires. Bedell (24) reported that in Manitoba, white spruce seemed to require a mineral seed bed and to reproduce well only on burned soil. Millar (242) also reported that white spruce reproduced following fire, especially on slopes. Hesselman and Schotte (146) and Nilsson (254) reported that in heaths in Europe, spruce species were slow to re-establish themselves after fires. Similar observations in North America were made by Breitung (38) and Minckler (243).

SUMMARY

In nearly every section of the preceding review, apparent contradictions as to the effect of fire can be found. These divergencies indicate that it is impossible to draw many general conclusions as to the ecological effects of fire. Rather, each combination of region, climate, forest tree association, soil type and plant species must be considered individually. However, the following points seem to be generally true:

1. Fire has been frequent in forest, shrub and prairie land for many

centuries, and has undoubtedly been a major factor in determining the direction and rate of plant succession.

2. In most cases, extensive, severe fires increase erosion by lowering the ability of the topsoil to absorb and retain water.

3. The ultimate effect of the changed moisture relationships on the water table apparently varies with different conditions and has not been investigated completely.

4. The temperature of the top soil during fire varies greatly, but below two inches the temperature rise is not great. There are some reports that this heat causes direct changes in the texture and chemistry of the soil as well as direct stimulation or inhibition of plant germination and growth.

5. Very frequently, by removing the insulating plant life or blackening the surface of the soil, burning results in greater post-fire soil temperature extremes for some time after the fire. These extremes may affect plant growth.

6. Reports of the effect of fire on soil productivity range from decreased plant growth to greatly increased growth, and each must be considered individually.

7. The acidity of the soil is usually lower after fire. Generally there is also increased soil calcium, phosphorus and potassium, but reports regarding increase and decrease in nitrogen are contradictory. Burning usually stimulates biotic nitrogen fixing activities in the soil.

8. Fire frequently results in an increase in moss, lichen and liverwort cover, certain species being characteristic of burned areas.

9. Fire influences the spread or destruction of numerous insect pests and plant disease organisms. Here again, each case must be considered individually.

10. Definite patterns of post-fire plant succession exist, but these are different for different sites and conditions.

11. A vigorous regrowth of herbs, grasses and shrubs occurs frequently the first few years following fire.

12. The effect of fire on tree reproduction varies with species, largely because of different methods of seed dispersal, seed survival, sprouting capacity and seedling requirements.

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THE CLIMAX CONCEPT

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Introduction 535

Climax Concepts 535

Discussion and Conclusions 538

Summary 543

Bibliography 543

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INTRODUCTION

Climax is a concept that is familiar to all plant ecologists; indeed, it is almost as old as the science of plant ecology. There has been, and is, considerable disagreement among leading ecologists concerning the definition of "climax", or whether the term has any practical value. To quote Whitaker (42), "no completely rigorous definition of the climax and its distinction has been found and apparently none need be expected." Nevertheless, climax is a popular ecological concept.

All of the following definitions may be found in current textbooks of ecology: Climax is the development of vegetation and the formation of soil toward a definite end point determined and limited by climate (3); climax is synonymous with a vegetational formation; it is the ultimate terminating community, determined by climate (41); climax is a terminal community of succession which is controlled by climate; it is capable of reproducing itself and may not be replaced by other individuals as long as the climate remains the same (29). climax is the final or stable community in a successional series; it is self-perpetuating and in equilibrium with the physical habitat (28). Upon initial inspection, these definitions appear to be compatible. However, an examination of the details reveals a severe rift in basic assumptions (21).

CLIMAX CONCEPTS

Historically, Hult (1885) was credited by Clements (8) as being the first to grasp the significance of climax. Graebner (1895) made the first comprehensive study of a great climax or subclimax community. Clements cites Warming (1885) as being the first to note what he calls the "universality of change", but Kerner (10) in 1863 had noted and described successional processes of several community types in the vegetation of Hungary. Schimper in 1898 (35) discussed vegetation, making a distinction between the influences of climatic and edaphic factors. With this work as a background, ecology in Europe developed on the basis of vegetation as a static entity. The American contemporary ecologists were developing the "dynamic" approach to plant ecology, which was initiated separately by Cowles (13) and Pound and Clements (32). In his description of the "Vegetation of Chicago and Vicinity", Cowles (14) made reference to "progression and retrogression". Succession was said to be controlled by climate over large areas, and by soil or edaphic factors in small areas. Braun-Blanquet (3)

concurs with this statement. Lippmaa rejects distinction between climatically determined and edaphically determined communities, since all communities are determined by both (42). In spite of the controversy that Clements' (7) monoclimax theory precipitated, this concept has been a strong influence on ecological thought for almost half a century. Clements postulated that climax developed through a certain successional pattern to the "highest type" which is synonymous with a "formation", a unit of vegetation determined by climate. He identified the formation with certain primary characteristics: climax dominants must represent the same life-form, dominants of related associations must belong to a few common genera. The association was termed an organism displaying the properties of life, birth and death. Areas within the formation which did not conform to the climax "type" were designated "disclimax," "preclimax" or "postclimax" with reference to vegetation on disturbed sites, dry sites or moist sites, respectively. Whitaker (42) reports Gams and Du Rietz as opposing the single climax while noting the resemblance of the theory to that of the Zürich-Montpellier group. He points out that although the latter group recognize a single climatic climax in a region, permanent communities maintained by other factors of the environment may be present also.

Ecology in Britain was greatly influenced by Clements. Tansley (38) adopted Clements' terminology of association, consociation, faciation, etc., and recognized their counterparts in developing vegetation as facies, associes and consocies. As a result of having studied in a country where historical aspects were manifest in ecology, Tansley was aware that certain biotic influences were capable of maintaining the vegetation in an apparently stable form. Similar to Clements, Tansley called these exceptions "subclimaxes" but differed in that he considered each one a specific climax, i.e., edaphic climax, physiographic climax, biotic climax (pasture or rodents), anthropeic climax (maintained by human activity), plagioclimax (succession deflected into a new course and so maintained in equilibrium e.g. sheep). Thus Tansley became a proponent of the polyclimax system. With reference to the character of the climax unit, the association, Tansley became the link between continental Europe and the Clementsian school of North America. In referring to Clements' association as an organism, Braun-Blanquet (3) called it a "flight of imagination". Tansley bridged the gap and called it a "quasi-organism". Tansley contributed the essential distinction

between autogenic and allogenic succession which refers to succession initiated by the internal factors of the environment (reactions of organisms) and the action of the external factors. Working in Tanganyika, Phillips (30) was a vociferous exponent of the Clementsian system. He was in complete agreement with all of Clements' principles and nomenclature. Although initially hesitant about accepting the concept of an association as an organism, Phillips (31) eventually adopted it on the basis of his belief in Smuts' theory of "holism". When applied to any group of individuals, the theory assumes that the properties of a whole cannot be predicted from the sum of its parts, the stress being placed upon the emergence of the new. Since physico-chemical factors may influence the rate and precise direction of succession, Phillips (30) proposed the adoption of such terms as "succession-acceleration" and "succession-retardation", with the final stage being designated as "succession-termination".

A theory which is almost the antithesis of the "association as an organism" concept is expressed by Gleason's (22) individualistic concept. It states that an association consists of communities, no two of which are precisely alike and are therefore unclassifiable into a definite association type. This concept is not in disagreement with Egler (20) or Curtis and McIntosh (17). Egler considers the term "climax" too nebulous to be used in his paper on Hawaiian vegetation. The vagueness of the term is illustrated by Whitaker (42) who lists 35 terms containing the word "climax", ten of which were introduced by Clements.

Stanley Cain has often assisted in the clarification of various climax theories to other ecologists (4, 5). He expressed his own views (6) when he said "since true climax can develop only on a medium site, it seems that the linking of all stable communities to the climax is highly hypothetical and serves no useful purpose." This idea was first expressed by Domin (19). Daubenmire (18) expresses a similar opinion. He states that climatic climax may be found only on a moderately drained, undulating topography. He adds that edaphic climaxes differ from climatic climaxes, and in a recent statement he intimated that there may be as many vegetational types as there are soil types.[1] Daubenmire bases climax units or associations on synusiae or unions whereby the communities are delimited on the basis of distinct combinations of plant unions which may or may not be of different life

[1] AIBS Meetings, East Lansing, Michigan, September, 1955.

form. Nichols (27) believed that the climax association type could be arrested by edaphic influences at a point far short of climax, but in general agreed with the climatic and physiographic approach of Cowles (26). Cooper (11), with remarkable insight, likened climax to a slowly moving braided stream formed by the merging of the streamlets and occurring when all factors—climatic, physiographic and reactional—are producing a minimum of change.

Neither the monoclimax or polyclimax system of classification is applicable in the tropics because of the tremendous floristic complexity of the vegetation. Indeed much of the taxonomy of tropical vegetation has not been worked out. Richards (34) found that there may be as many as 100 species per acre in tropical forests. His climatic types occur on zonal soils, while the term "azonal" indicates special conditions of soil and topography supporting a stable community. Introducing a different approach, Randall (33) compared autecological attributes of pioneer and climax forest communities. Statistically significant differences were found in the representation of certain morphological, physiological and life form characteristics.

Curtis and McIntosh (17) classified upland forest stands of northern Wisconsin, using the established method of leading dominants. Fifteen separate groups were obtained when stands were classified on the basis of one leading dominant, 105 groups on that of four dominants. When each species was expressed as an importance value derived from a summation of relative density, frequency and dominance, and was weighted by an adaptation number, the entire group formed a continuum with species matching all segments of the full environmental range of the region. No large group was aggregated to the same environment and no environment was devoid of adapted species.

Whitaker (42), after a comprehensive literature review consisting of some 700 references, introduced the "climax pattern hypothesis", which is a gradient analysis of natural communities in terms of population distributions among environmental gradients. He considered this to be a more realistic approach than either the mono- or polyclimax theories. He presented the prevailing climax as a definable abstraction to replace the undefinable climatic index. Prevailing climax was suggested as the vegetation type which occupies the most area.

DISCUSSION AND CONCLUSIONS

Although the initial definition of climax in use in current textbooks appears to be clear cut, it harbors undertones of infinite variability in

current climax theory. The various ideas expressed in climax theory testify to the tremendous variation involved in a definition of climax. This is expressed in any divergence from the monoclimax theory where there is insistence that environmental factors, in addition to climate, maintain stability. Cooper (11) early recognized the complexity involved when he likened succession to a braided stream. Gleason (22) considered the complexity insurmountable when he said "vegetation is so diverse that it cannot be classified." Whitaker's climax pattern appears to be based on diversity, while Curtis' continuum expresses it. Clements, however, was not unaware of this diversity and in a letter to Phillips (31) referred to climax as a veritable mosaic. The main rift between the concepts of monoclimax and polyclimax is not the existence of physiographically- or edaphically-stable communities. Clements recognized these exceptions with the introduction of the terms "subclimax" and "postclimax" into his theory. The rift occurs either in the assumption that, given sufficient time, climate is the overall controlling factor of vegetation, or in the length of time considered adequate for stabilization to occur. If time were considered on the human time scale (34), it is conceivable that it would be insufficient for the manifestation of climate. To assume eventual control of the environmental effects of soil texture, edaphic factors and particularly topography, Clements must have considered time on a geological scale, with the assumption of eventual erosion to base level. This assumption may be immediately questioned on the grounds that with a few exceptions (Australia), peneplanation in the geological development of the earth has rarely been achieved (25). However in South Australia, Crocker and Wood (15) cannot accept climate as an overall controlling factor because the vegetation appears to be dominated by soil and edaphic influences. This makes Clements' position regarding climax even more difficult.

Phillips (31), who professes to agree with Clements completely, declares that the monoclimax concept assumes that a uniform climate has the power to transform edaphically different habitats into one uniform climax. Clements' complicated nomenclature concerning succession and amalgamation of units from seral to pan-climax and contemporary divergence as a result of various disturbances, is almost as complex as the processes themselves. For this reason, even his supporters (12, 24) avoid using many of his terms. The fact that Phillips (30) invented the term "succession-termination" to describe

apparently stable vegetation suggests that he was dissatisfied with the lack of descriptive precision of Clements' proclimaxes. This same dissatisfaction provoked the development of a host of climaxes associated with the polyclimax theory. This has contributed greatly to confusion in ecological theory (42). Upon initial examination it would seem advantageous to utilize such binominal nomenclature to indicate the type of diversion from climatic climax. Its value, however, is limited, since almost infinite variation exists in each of the binomials. For example, in a biotic climax due to grazing, the status of the vegetative cover depends upon the severity of the grazing. Similarly, the status of a fire climax is dependent upon the frequency and severity of the burning. The binomial sets no standard of disturbance that can be recognized.

With reference again to the monoclimax theory, various other points have been questioned. Cain (6) criticizes Clements' undefined "highest type" in the attainment of climax. Clements' insistence that the dominants in a formation represent the same life-form, although apparently valid in American grassland, does not apply in the lake forest. Hemlock, in addition to maple, is considered a climax species in the lake forest of North America (3a, 37). Consequently Clements' idea of life-forms has led to misrepresentation of climax species in the area (41).

Whitaker (42) discusses the relative merits of monoclimax and polyclimax and favors the latter because it is free of the assumption of convergence, in spite of differences in environment, and free of a subjective choice of a climatic climax. The polyclimax idea permits study of actual successions to climatic associations with some realism while retaining the community unit assumption. This results in the confusion provoked by a tremendous number of climaxes. Whitaker feels that the climax pattern hypothesis is the basis for research of gradient analysis, permitting direct relation of environmental gradients of the whole diversity of climax stands in a whole range of environments. Any term such as "climax" which is so diverse as to be undefinable has questionable value. For practical purposes in field ecology a climax appears to be rarely if ever attained, and is influenced by such a host of nebulous factors that it is even questionable theoretically. Nearly all ecologists in the field concur that succession occurs, indeed that a trend toward mesophytism in succession is evident. That the trend is "terminated" is not a proven fact.

Climate varies particularly in the temperate regions, not only during geological time but during shorter periods (27). These short-run climatic influences have a very real effect on the vegetation, as was witnessed in the Great Plains during the drought of the 1930's (39). More than a decade has passed since that disturbance, but it will take a long time for the mixed prairie to return to true prairie (40). These departures from the mean in the climate of the Great Plains cause retrogression in the development of vegetation. Study of the regeneration of the prairie indicates that a considerable period of time is required for the prairie vegetation to reach equilibrium with the climate, and that the climate is likely to change again before this equilibrium can be reached. The prolific number of relicts which Clements (9) apparently found suggests that vegetation often lags behind the climate and in reality probably never catches up. This lag would be accentuated for long-lived woody species. Unless the climatic change were very extreme, it would not significantly alter the forest composition until the existing generation of trees had died. A forest may well be more typical of the climate of a century previous than it is of the climate of the day. Historically, climate has a tremendous effect on the vegetation. The deciduous forests of the southeastern United States are richer in species than those of Europe (2), mainly because those in America escaped Pleistocene glaciation. Some of the sub-tropical mesic species could probably thrive in the Caucasus (2) but are absent because the east-west range of mountains prevented escape of the forest from the advancing Pleistocene ice. Beech forest in England was completely killed out in Pleistocene times, but since its re-introduction, presumably by man in 2000 B.C. (38), it has continued to thrive and reproduce. There may be tolerant species in other parts of the world which are capable of reproduction and more efficient utilization of the environmental resources of temperate regions of North America than those which are now present. For example, *Euphorbia esula,* an introduced forb, is capable of invading undisturbed Mixed Prairie grassland in Saskatchewan. Perhaps species which were destroyed during periods of glaciation would be better adapted in the present climate than species of the present day. It is possible that insufficient time has elapsed since the last glaciation for climax species to migrate or evolve. It seems logical to assume that if the redwood forest of California had been destroyed during the last ice age, insufficient time would have elapsed for succession to replace it. The decrease in size of populations

by glaciation may have decreased the genetic diversity and subsequent evolutionary capacity of certain species.

The tropics are well known for their great floristic diversity (34). Tropical regions presumably have had continuous uninterrupted development from the Carboniferous period in which to evolve their present diversity. Existing climates prolonged for similar periods of time in the temperate region would probably permit the evolution of a flora much more diverse than it is today. It is likely that temperate vegetation will have become more complex before the advance of the next glacier.

Whitaker's (42) "prevailing climax" in relation to maximum area covered may be criticized on the basis that a comparatively minor constituent of the mature community in certain areas can be well represented in the understory and therefore becoming a leading dominant of the next generation. The fact that the species is dominant in small areas only suggests that under the existing climate, dominance over the major region may not occur for several generations. This may possibly apply to beech forest in Michigan. Since existing vegetation is moulded by the interaction of climate and the numerous factors of the habitat, all of which are continuously changing; since the time lag of vegetation behind climate and environment is surely to increase with the longevity of the species; and since capacity for immigration and evolution of the species and the history of the area are all important factors to be considered, the prediction of a climax vegetation or the reference to vegetation as having attained an endpoint appears to be presumptuous. It would be advisable to avoid terms which denote a degree of finality in succession. It has been suggested that a more realistic and less confusing approach would be to refer to existing vegetation as pioneer, intermediate or most advanced. A prediction, if possible, of the next stage in succession also would be helpful. Selander's (36) definition of climax (communities which represent time phases of great stability in which successional causes cannot be observed and the future cannot be predicted) would appear to fulfill this requirement.

With reference to the study of plant communities, there are those (1) who believe that the Braun-Blanquet approach lends itself to world-wide application. Curtis and McIntosh (17) with their continuum approach, have shown that populations of species reveal a continuous overlapping of presence and magnitude entirely opposing

classification into discrete units. In addition to Wisconsin forests (3a), the continuum may be applied to prairie (16), to cryptograms, (23) and to certain forests of Idaho and Switzerland[2]. Considerable research is necessary in various parts of the world, particularly in the tropics, to reveal the universal applicability of ecological approaches developed in different types of vegetation. The continuum approach is one which reveals the pattern in the complexity of vegetation and would appear to be applicable to most vegetational units. The tremendous species diversity in the tropics and the difficulty involved in their identification may make application of this method too laborious. Comparison of attributes of vegetation representing pioneer and terminal stages of existing succession (33) requires considerable research for its assessment. The same may be said for the physiognomic approach of the tropics (34) in its application to temperate vegetation.

Research activity should be concentrated on concepts which suggest the possibility of universal application. The development, verification and acceptance of a unified ecological philosophy would provide the impetus required for the firm establishment of plant ecology as a world science.

SUMMARY

Textbook definitions of climax reveal a severe rift in basic ecological assumptions. The monoclimax theory is not workable in all vegetation types. The polyclimax theory is limited because it does not recognize the geological time scale, and because its numerous terms lack precision. The prevailing climax may be critized, since a minor constituent of forest understory may become a leading dominant of the next generation. A definition of climax should avoid terms which denote "finality" in succession. Research should be concentrated on concepts which suggest universal application. The development, verification and acceptance of a unified ecological philosophy would provide the impetus required for a firm establishment of plant ecology as a world science.

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BIOLOGICAL ANTAGONISMS DUE TO PHYTOTOXIC ROOT EXUDATES

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Early Work 547
General 547
Methods of Study 549
Excreted Substances 551
Exudates of Woody Plants 552
Exudates of Grasses and Herbs 554
Interactions of Higher Plants and Microorganisms 555
Ecological Considerations 556
Discussion 558
Bibliography 559

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Phytotoxic and phytostatic compounds kill or inhibit the growth of plants. Synthetic compounds of this type are often used as commercial weed killers. Less known, and more poorly understood, are the natural toxic substances which are excreted from the roots of higher plants or derived from their detritus. This paper reviews the literature discussing hypotheses or investigations of these compounds and ecological phenomena that may be pertinent.

EARLY WORK

Throughout the nineteenth century there was a steady trickle of papers and theses concerning root exudates. DeCandolle (1832), the French botanist, said that "... the excretions of roots, although poorly known, undoubtedly play a very important role and merit better attention." Way (1847) associated the formation of mushroom fairy rings with the presence of toxic substances in soil.

Since the turn of the century, phytotoxic or phytostatic substances have been the subject of numerous investigations and discussions. In this country the work of the group led by Schreiner and Reed dominated the scene (Schreiner and Reed, 1907, 1908, 1909; Schreiner and Shorey, 1909, 1910; Reed, 1908). In England many studies were carried out by Bedford and Pickering (1903, 1911, 1914, 1919), and a sizeable body of literature has accumulated in Germany, France and other countries (Lilienfeld, 1905; Molliard, 1915; Bode, 1940; Guyot, 1951; Maze, 1911; Aberson, 1909; Klaus, 1939; Kaven, 1930; Ollech-Steglitz, 1912; Kohn, 1899; Vogel, 1929; Vogel and Weber, 1931; Lumiere, 1920; Kaserer, 1913; Bronsart, 1949), so that interest in the problem is more than local or regional in character.

GENERAL

Preston et al. (1954) have offered rather conclusive evidence that at least some species of plants exude substances that are subsequently absorbed by roots of other plants. They introduced alphamethoxyphenylacetic (MOPA) acid into the stem and leaves of bean plants by several methods. Within nine hours the MOPA was detectable in untreated plants that were growing in the same pots as treated ones.

Some toxic plant products have well-known beneficial effects. For example, the red pigment in onions, when present, blocks the entrance of the smudge fungus *Colletotrichum circinans* (Walter et al (1929).

The specific compound seems to be protocatechuic acid. Small concentrations of other organic acids have also been shown to inhibit the growth of plants (Hildebrandt et al. 1954). Enough HCN was excreted from the roots of flax to retard the growth of several species of pathogenic fungi (Timonin, 1941). However, some plants produce toxic decomposition products (Gries, 1943) whose effects may be difficult to distinguish from those of direct excretions from living roots. Environmental conditions are important in this respect, for fungi growing under poor nutrient conditions are susceptible to toxins (Wood and Tveit, 1955). Kug et al. (1955) found that fungistatic substances may be exuded only when the outer tissues of roots are injured or removed. Responses have been produced in extracts of diseased tissue (Allen, 1954). It may not be possible to determine whether the substances are fungal or radical in origin.

"Soil fatigue", a catch-all term used when soil is no longer productive, has sometimes been ascribed to root excretions. Pantanelli (1926) believed that soil sickness may develop when root excretions prevent the development of necessary soil microorganisms. Beneficial bacteria may disappear because of antagonistic organisms (Demolon and Dunez, 1935). Schreiner and Sullivan (1909) showed that unfavorable soil conditions may be caused by "organic substances arising through crop growth." Mader (1947) found that some types of soil-sickness may persist even after sterilization of the soil. Unfavorable conditions that precede toxic root excretions may include oxygen deficiency (Livingstone, 1923), which can be caused by poor soil structure.

Various methods have been used to ameliorate the effects of toxic agents. Johansson (1936) used a chemical soil sterilizer to overcome the deleterious effects of fruit trees where such trees had been previously grown. Fertilizer salts seemed to render some harmful organic substances inactive (Schreiner and Skinner, 1912). Hartwell et al. (1927) reported that liberal applications of lime and phosphorous helped overcome the influence of crops on those which followed. There was evidence that only a change in hydrogen-ion relationship was needed. In a water culture study, Prianischnikov (1914) used carbon to absorb toxins.

Abundant literature denies the existence of growth-inhibiting root exudates. The objections are both general (Loehwing, 1936; Miller, 1938; Thatcher, 1923) and specific. The strongest arguments come from investigators who believe that the large amounts of carbohy-

drates from plant residues cause abnormal competition for nitrogen between plants and soil bacteria or other microorganisms (Meyers and Anderson, 1942; Shrikhande, 1936; Dutt, 1935; Albrecht and Allison, 1931; Loehwing, 1937; Conrad, 1932). The possible depressing effects of added high-carbohydrate residues have been duplicated by adding dextrose (Doryland, 1916). This temporary exhaustion of nutrients has been appropriately termed "biological absorption" (Akhromeiko, 1932) and is most tenable when applied to plants with a relatively high carbohydrate residue, such as sorghum (Conrad, 1927; Conrad, 1928). However, some investigators have failed to find a significant association between specific microorganisms and the appearance or disappearance of root injury (Cochrane, 1948).

Apparent toxic effects of roots or residues may sometimes be due to an accumulation of residual spray chemicals (Verner, 1937; Childers, 1941). This is probably most often true when arsenic has been used for several years.

Changes in acidity have sometimes been associated with soil toxicity. Plants that produce "more acidity" would have a high cation-exchange potential and readily absorb calcium and magnesium (Burgess, 1925; Groh, 1926). Differences between competing plants could result in mineral-nutrient starvation of one of the species under these conditions. Toxic root exudates have been suspected in some soils, whereas nutrient depletion by previously grown crops having a high mineral requirement may provide a more logical answer (Hartwell and Damon, 1918; Hartwell et al., 1919).

A more recent explanation of root growth inhibition deals with blocks of the respiratory system due to enzymatic depletion (Lafond, 1951). Cold-water extracts of humus from a poorly growing stand of jack pine increased the respiration of a homogenate of jack pine root tips immediately. This was interpreted as indicating a breakdown of the decarboxylases of the roots and resultant depletion of this enzyme system.

METHODS OF STUDY

Phytotoxic exudates have been studied most often by use of water extracts (Cochrane, 1948; Osvald, 1947; Winter and Sievers, 1952; Prat and Retovsky, 1944). In this method, plant parts are chopped into pieces, or blendorized, and soaked in distilled water for periods up to several days. The water is then filtered to remove solid matter, and used to water plants growing in pots. The degree to which growth of the

potted plants is depressed indicates the toxicity. It should be pointed out that the phytotoxic material obtained in this manner is not necessarily exuded under normal growing condition. It may, however, approximate the substances released on decomposition of dead roots. Water extraction and alcohol extraction have been used to separate different phases of a toxic system (Proebsting and Gilmore, 1941). Bennett and Bonner (1953) obtained highly concentrated extracts of toxic substances by blendorizing tissues, filtering to remove cell debris, centrifuging to remove small particles, and freeze-drying to obtain a powder.

Leachings from pot-grown plants can be used to assay toxicity (Bedford and Pickering, 1911; Bonner and Galston, 1944). With this method leachate from plants grown in sand is used to water other plants grown in sand with ample mineral nutrients and water for growth. This approach would seem more desirable than the water— or alcohol-extraction method because the exudant, if present, is obtained from uninjured normal roots, and it is not necessary to prepare a fresh water-extract every day.

Long et al. (1956) studied the leaching of radioisotopes from leaves. Their method would seem useful in studying root excretions also, especially those comprised of inorganic substances.

It may be desirable to grow plants in a nutrient solution, subsequently watering plants in pots with this solution (Maze, 1911; Livingstone, 1907; Minina, 1927). If the plants in the nutrient solution exude a material, growth of test plants watered with this solution should at least be retarded. Here, again, arises the problem as to whether plants in water culture are physiologically similar to those growing in soil. Using water and sand culture methods, Muller and Muller (1956) found three species of plants to contain growth inhibitors—*Franseria dumosa, Thamnosma montana, Encelia farinosa.*

Growing plants in close proximity may be useful for detecting toxic substances in preliminary stages of study (Ljubic, 1955).

Exudation of nucleotides from excised pea roots was ingeniously studied by Stenlid (1947) who measured the extinction of ultra-violet light by exudate in the surrounding medium. Prat (1933) used polarigraphic methods to determine the substances.

For conclusive work, even the most carefully controlled bioassays should be followed by isolation and characterization of the phytotoxic substance. Rovira (1956) has used paper chromatography in studying

exudates of oats and peas. This seems to be a highly satisfactory method of analyzing root exudates.

EXCRETED SUBSTANCES

Many plant families have a member that is known or suspected to produce phytotoxic root exudates. The exudates include widely divergent groups, e.g., oils (Schuphan, 1948), antibiotics (Winter and Willeke, 1952; Wright, 1951), sugars (Patrick, 1955; Brown et al., 1950), coumarin (Veldstra and Havinga, 1943), alkaloids (Mothes, 1955; Mukerji, 1920), thiamin, biotin (West, 1939), mineral salts (Frey-Wyssling, 1930; Achromeiko, 1936), enzymes (Lyon and Wilson, 1921; Livingstone, 1909) aldehydes (Gray and Bonner, 1948), nitrogenous compounds (Ludwig and Allison, 1940), ammonia (Prianischnikov, 1928), nucleotides (Lundegardh and Stenlid, 1944), amino acids (Andal et al., 1956; Parkinson, 1955) and nucleic acid derivatives (Fries and Forsman, 1951). At times the quantity of material exuded seems to be a function of the environment. For example, Katznelson et al. (1954; 1955) found that wetting and drying cycles cause the liberation of much more amino acid than is usual under steady soil moisture conditions.

Early workers attributed the effects of apparently toxic substances to "organic substances" (Molisch, 1887; Collison, 1925; Livingstone et al., 1905). Still other investigators believed that organic acids were the toxic agents, but failed to identify them further (Kunze, 1906; Ratsek, 1934; Pfeiffer and Blanck, 1912; Coupin, 1917; Haas, 1917; Odland and Smith, 1933; Odland et al., 1934; Hartwell et al., 1919). Specific acids suspected included oxalic (Czapek, 1896), dihydroxystearic (Schreiner and Lathrop, 1911), salicylic (Collison and Conn, 1925), cinnamic (Bonner and Galston, 1944), chlorogenic (Politis, 1948), melilotic, phenylpropioloc, piperic and 2-furanacrylic (Prill et al., 1949). Only in relatively recent years have the detailed composition and structure of these compounds been intensively investigated. For example, juglone, the toxic principle from walnut trees, has been proposed as a fungicide (Gries, 1943).

That organic nitrogen compounds, including amino acids, are excreted into the rhizosphere is a fact well established (Virtanen, 1947; Virtanen and Laine, 1935), but the amounts may not be great (Wilson and Lyon, 1926; Ludwig and Allison, 1940). There is evidence that proteolysis takes place especially fast in wilting grass and

that the degraded protein reappears in part as amino acid (Kemble and MacPherson, 1954). This could be, in part, the explanation for depressed yields of corn in dry years as noted by Wilkins and Hughes (1934).

Positive identification of these compounds as substances present in or derived from roots does not assure that, under normal conditions of growth, they are excreted into the rhizosphere. In at least some cases they may be attributed to breakdown of portions of the root (Katznelson et al., 1948; Russell, 1950).

EXUDATES OF WOODY PLANTS

Exudates, often toxic, have been found or proposed for a wide variety of woody plants, including citrus (Martin, 1950), chinquapin (Offord, 1952), guayule (Bonner, 1946), greenleaf manzanita (Sampson, 1944), ponderosa pine, redwood and Monterey pine (Daniel, 1949). Both seedlings and mature trees may be responsible.

Replanting peach trees on old peach-orchard sites has been a problem for many years in all regions that produce this fruit. Upshall and Ruhnke (1935) attributed the poor success of sequent peach orchards to a "depression of nitrification from the decomposition of the peach roots." Proebsting and Gilmore (1941) found that peach roots added to virgin soil inhibited the growth of peach seedlings. Proebsting (1950) later noted that fumigation gave a partial remedy. Different investigators have suggested that toxicity may be due to nutritional disturbances, toxic agents, nematodes, spray residues and insects (Koch 1955). Recently, Patrick (1955) concluded that microbial action on the amygdalin (a glycoside containing cyanic acid) fraction of peach roots is mainly responsible for the toxic factor in old peach orchard soils. Fungi are associated with the release of the toxic agent (Wensley, 1956). Ward and Durkee (1956) observed that not all varieties of peaches produce enough of this substance to be toxic. The latest research indicates that nematodes may play an important part (Mountain and Boyce, 1958), perhaps by providing infection courts for bacteria and fungi, or by stimulating the production of toxins in the roots.

Extracts of black locust (*Robinia pseudoacacia*) and basswood (*Tilia planifolia*) hindered the growth of barley roots (Waks, 1936). Perry (1932) also found that black locust had phytostatic effects on pine roots.

Leaves of some woody species have been definitely shown to produce toxic substances. In 1942 Went observed that there were five times as many annual herbs of some species under dead *Encelia farinosa* bushes as under live ones. He attributed this to the production of specific substances by the living shrubs. Gray and Bonner (1948) subsequently identified the phytotoxin as 3-acetyl-6-methoxybenzaldehyde. They also found that the toxic effect of *Encelia* leaves is less striking on plants in a good garden soil than in sand culture—an indication that the toxic agent is inactivated or destroyed by the microflora of the soil. Muller (1953) suggested that the failure of plants to grow beneath *Encelia* might be attributed to the short life span of this species and to the fact that it does not modify the site enough to be a factor in succession. Foliage of *Artemisia absinthium* also produces substances that hinder the development of other species (Funke, 1943; Bonner, 1950).

The phytotoxic effects of *Juglans* have often been observed. The first note in the literature seems to have been made by Stickney and Hoy in 1881. In 1903 Jones and Morse noted the absence of cinquefoil close to butternut trees in fields overgrown with this herb. They reported that "each large tree occupies the center of a clear grassy circle of a diameter considerably exceeding the farthest spread of its branches." Cook (1921) observed the wilting of potato and tomato plants growing in the immediate vicinity of black walnut trees. He observed that plants wilted but did not lose color and die as when attacked by fungi. Schneiderhan (1926), Massey (1925) and Perry (1932) recorded the antagonistic effects of walnut trees on pine trees, alfalfa, tomato, potato, apple and corn.

Walnut was one of the first woody species from which a specific toxic agent was isolated. Davis (1928) identified the toxic constituent of walnut roots and hulls as juglone. The purified and crystallized extract of this substance produced toxic symptoms when injected into tomato and alfalfa plants.

Tree seedlings have been shown also to retard the growth of grasses (Jensen, 1907) and of other trees. Ljubic (1955) grew many combinations of seedlings in crowded plots and found that *Quercus robur* antagonizes *Fraxinus pennsylvanica*, while *Ulmus parvifolia* antagonizes *Quercus robur*. He also noted that seedlings and trees often interacted differently, with the strongest effects coming from seedlings. The reason may have been that the young roots of seedlings are highly concentrated

and have a relatively thin suberized covering. In this respect, Gyllenberg and Hanioja (1956) observed that bacteria requiring certain free amino acids may be found around root hairs but not around the suberized older roots.

EXUDATES OF GRASSES AND HERBS

The maleffects of grasses on trees was demonstrated by Pickering (1917, 1919) and by Howard (1925). Although subsequent writers are not entirely in agreement with their hypothesis that these effects were due to toxic excretions, Russell (1935) has pointed out that their evidence has never been examined sufficiently.

Pure stands of bromegrass often reach a "sod-bound" condition. Benedict (1941) states that, while the cause may be over-dense root growth and resultant nitrogen deficiency, the accumulation of growth-inhibiting substances would also be favored under these conditions.

The depressing effect of sorghum on succeeding crops has been studied by a number of investigators. Breazeale (1924) believed it to be due to the presence of "a toxic body formed during decomposition of the stubble." Later investigators (McKindley, 1931; Wilson and Wilson, 1928) attributed this effect to the large amount of raw carbohydrate added to the soil and a resultant unbalance in the C/N ratio. The effects of the added stubble seem to disappear within a few months (Hawkins, 1925; Breazeale, 1924). Regardless of the cause, sorghum seems to have a stronger depressing effect on winter wheat than does corn (Sewell, 1923).

Other grasses have also been suspected as toxin-exuders. Rye apparently retarded grape plants even when soil moisture and fertility were excellent (Cubbon, 1925). Fletcher (1912) believed that corn roots exuded toxic substances. Kommendahl (1957) found that quack grass rhizomes contain a substance that inhibits the growth of alfalfa seedlings. The rhizomes were dried, ground to powder, sterilized, and mixed with soil in greenhouse pots.

Phytotoxic root exudates have been claimed for a wide variety of herbaceous plants, including peas (Molliard, 1913), alfalfa (Pouget and Chouchak, 1907), lupine (Prianischnikov, 1934), zacate, rice (Peralta and Estioko, 1923) and sesame (Skinner, 1913) as well as weeds such as *Hieracium and Solidago* (Becker, 1951; Becker and Guyot, 1951). There are no indications that one particular plant family is especially important in this respect. Skinner (1913) pointed

out that these effects are "more or less specific, affecting one kind of plant whereas another kind of plant is practically unaffected." For example, flax, which is suspected of exuding toxic substances, should not be planted after flax crops, but grains or legumes may be planted after it (Becquerel and Rousseau, 1941).

Aqueous extracts of field bindweed and of Canada thistle inhibited growth and germination of flax and wheat seedlings (Helgeson and Konzak, 1950). Increasing the concentration of phytotoxic solution progressively decreased germination and growth. It is probable, however, that all of the substances found in an aqueous extract will not be present under normal growing conditions.

Ahlgren and Aamodt (1939) noted harmful interactions between grasses and legumes and pointed out a need for basic studies. Such interactions might have a qualifying influence on range management planning.

INTERACTIONS OF HIGHER PLANTS AND MICROORGANISMS

Starkey (1929) suggested that the effects of root exudates may be important to the biological balance of soil macro- and microorganisms, a view which more recent workers (Becker et al., 1951) have taken also. "Sick" or "exhausted" soils may merely be microbiologically inefficient under certain systems of cropping. Such problems may be of great importance in forest stands where one crop is grown perpetually (Waksman, 1937). They may have special significance in the "breakdown" of pure stands planted on sites where the species does not naturally occur.

In some of the earlier investigations (Grieg-Smith, 1911) bacteria were found to produce toxic exudates. While this has never been disproven, more recent work indicates that bacteria may be important as competitors for nutrients, especially when free carbohydrates are abundant. Bacteria may also render certain root exudates ineffective (Muller and Muller, 1956).

Actinomycetes are among the various types of organisms which exude growth inhibitors. Meredith's actinomycetes have been found to inhibit the growth of fungi (Thaysen and Butlin, 1945). This phytostatic effect may have a bearing on mycorrhizal relations, even when there is no apparent actual damage to mycorrhizal fungi. It could be of extreme importance in tree nursery management.

According to Buxton (1958), substances exuded by roots can ap-

parently induce genetic changes in pathogenic fungi directly, rather than selectively, so that host selectivity is altered. Change in the range of available hosts is not uncommon in bacteria but is rare among fungi.

Mycorrhizae are thought to exude substances which exhibit a growth-promoting action on the host plant (White, 1941), repel pathogenic fungi (Garrett, 1950) and inhibit seed growth (Bokor, 1956). These may be important additions to the commonly ascribed functions of mycorrhizal fungi. Conversely, some fungi seem antagonistic to mycorrhizae (Levisjohn, 1957). Other toxic substances may be derived from the surface litter of a wide variety of tree species (Melin, 1946, 1948; Rayner and Neilson-Jones, 1944). These antagonisms and counter-antagonisms would make an interesting, although difficult, subject for study.

Some root exudates may also be helpful to soil microorganisms. Katznelson et al. (1948) suggest that the excretion of substances, such as potassium or phosphorus, may favor bacteria with simple nutritional requirements. Rovira (1956) found that root exudate stimulated the growth of Gram-negative bacteria. Gyllenberg (1956) noted that bacteria requiring pre-formed vitamins were stimulated by roots of grasses.

Even very young roots may, at times, seem to exude some sort of substance favorable to microorganisms. Timonin (1940) found 11 to 28 times as great a bacterial population in the rhizosphere of three-day-old seedlings as elsewhere in the same soil. Fungal populations were not increased as greatly. Even though sloughing off of the epithelial tissues of roots produced material that seemed to favor microbial development around older roots, there was no such material around the tips of three-day-old roots. This indicated that an exudate, not a decomposing root cap, stimulated bacterial growth.

Mineral soil itself, minus all organisms, is biologically active only to the extent of its surface area. In this respect Papadakis (1941) proposed that the clay colloids may be important in absorbing excreted compounds and keeping low the amount present in the soil at any one time.

ECOLOGICAL CONSIDERATIONS

The possible role of plant excretions in the natural succession and phytosociological order of plant communities has been discussed by many authors, including Bonner (1950), Varma (1938), Bedford and

Pickering (1914; 1919), Deleuil (1950; 1951) and Guyot et al. (1951). Guyot (1951) regards excretions as a factor of soil fertility, although this is not in keeping with present concepts. As for specific relationship, little is known. Mothes' (1955) statement is pertinent: "Totally unexplored is the question of the role alkaloids play in the soil into which they may be leached from the leaves or excreted by the roots. The possibility exists that they represent an ecologically important factor." Farrow (1917) noted the competition between *Pteris* and *Carex* and believed that the success of *Pteris* was due to the effects of a leachate from its fallen-over dead fronds.

Other ecological relationships may involve the effects of root excretions on fungi (Neilson-Jones, 1941), bacteria (Fletcher, 1907), microorganisms (Lucas, 1947) and seed germination (Becker et al., 1950; Becker and Guyot, 1951).

The importance of antibiotics in competition has been often discussed within the past few years. This interest has developed largely as a result of the discovery of bacteriostatic substances such as penicillin. Salisbury (1944) drew attention to the possible importance of these substances with respect to the plant competition problem. A few years later Brian (1949) observed that the production of antibiotics is a probable cause of antagonism between different groups of organisms. While it is difficult to get direct evidence that antibiotics are produced naturally by plants growing in the soil, these compounds have been found to be stable enough to have significant biological effect if produced (Jefferys, 1952). If antibiotics do not themselves have an antagonistic effect, they may cause a detoxification of excreted plant products (Nickell and Finlay, 1954). For example, the antibiotic activity of fungi (Wright, 1954; Wright, 1956) might permit plant associations which phytotoxic exudates might otherwise render impossible.

Cooper and Stoesz (1931) noted that colonies of *Helianthus scaberrimus* grow outward from a center of origin with the older parts dying after establishment; they are apparently subject to a self-exuded toxin. Each spring the developing buds "find themselves" in areas of fresh soil, with a fully developed root system ready for operation. In spite of the high mortality to which it is subject, the species thus maintains itself as a constant and characteristic member of the prairie community. Curtis and Cottam (1950) found peripheral effects in various genera of Compositae, including *Helianthus, Antennaria, Aster* and

Erigeron. They said that "Future students of interspecific relations, particularly those concerned with why certain species do not grow together, should explore the possible role of chemical substances in the competition between plants." Molliard (1913) had noted autotoxic effects of peas long before this. Contrariwise, Keever (1950) found no evidence that excreted substances changed secondary succession in any manner.

Muller (1953) claimed that, even though a potent toxic substance is produced by the leaves of *Franseria,* large numbers of shrub-dependent herbs are found around these plants. This he attributes either to the action of the microflora in breaking down the toxic substance or to absorption of the toxin by the colloidal components of the soil.

It appears that seed germination may be increased (Brown, 1946) or decreased (Osvald, 1949) by external substances supplied by adjacent roots. Especially interesting are the autotoxic effects of some species (Becker, Guyot and Montegut, 1951). Evenari (1949), who thoroughly reviewed the subject of germination inhibition, said that the presence of germination-inhibiting substances in plants seems to be a widespread phenomenon, occurring in all parts of plants—in fruit pulp, fruit coats, endosperm, seed coat, embryo, leaves, bulbs and roots. They are non-specific in their effects. Any plant which exudes a substance influencing germination is potentially a strong ecological determinant.

DISCUSSION

The statements of Thatcher (1923) and Bonner (1950) reflect some of the most progressive thinking on the subject of root exudates. Thatcher, in 1923, said, "Definite proof that observed injurious effects on a second crop are due to toxic chemical substances in the soil produced by or in association with the first crop has not yet been established." Nearly 30 years later, after much investigation and refinement of analytical methods, Bonner said that "the existence of plant toxic substances would seem to be better supported at present than it has been in the past." At the present time, sufficient evidence exists to assume that at least under some conditions, normal plants liberate phytotoxic exudates of ecological significance. In 1952, Shaw wrote, "the concept that specify toxicity of certain organic substances in soil has an adverse effect in plant nutrition has been scoffed at many times, but it has been adequately demonstrated by recent investigations." Martin's (1951) statement that "... biological order is actually based upon

disorder, upon antagonism," leads us a step further in our understanding of natural antagonisms. The part that exuded substances play, however, is as yet poorly understood.

Knapp (1954) and Grummer (1955) have discussed the effects of phytotoxic and phytostatic root exudates and their possible ecological effects. This phenomenon has generally received greater attention in Europe than in America, even though many American investigators have reminded their readers of the possibility.

The probable ephemeral nature of free toxins in the soil should always be remembered. These often complex organic substances are undoubtedly subject to rapid deactivation or destruction by soil bacteria and fungi. However, they may still play an important role in soil-organism interrelationships if production is sustained. It is hoped that this discussion of the subject will not be construed as an overemphasis but rather as cognizance of the possibilities.

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Genotypic Control of Chromosome Form and Behavior	H. Rees, *University of Birmingham, England*
Seedling Morphology in Applied Genetics and Plant Breeding	Gordon Haskell, *Scottish Hort. Res. Inst.*
Wild Plant Hybrid Frequencies	H. T. Clifford, *University of Queensland*
Chemical Tests in the Diagnosis of Plant Virus Diseases	R. C. Lindner, *Washington State University*
Techniques for the Observation and Isolation of Soil Microorganisms	R. D. Durbin, *University of Minnesota*
Cell Wall Organization in Higher Plants I. The Primary Wall	A. B. Wardrop, *Commonwealth Scientific and Industrial Research Organization, Melbourne, Australia*
Limnological Investigation Methods for the Periphyton "Aufwuchs" Community	Alena Sladeckova, *Department of Water Technology, Prahe, Czechoslovakia*
The Inter-Relations of Vegetative and Reproductive Growth in Plants: A Review of the Literature with Special Reference to Indeterminate Plants	E. R. Leonard, *Glasshouse Crops Research Institute, Littlehampton, England*
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